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Ecological Assemblages in a Warming Climate:

Addressing Knowledge Gaps in the Role of Thermal Heterogeneity and Realised Niches at a Global Scale

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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Ecological responses to Anthropogenic climate warming are occurring across the globe. The aim of this thesis is to critically examine knowledge gaps in: i) how assemblages respond to multidimensional temperature change; ii) patterns of realised niches across species' assemblages. I investigate these gaps to build the requisite knowledge to describe and predict assemblage scale responses to climatic warming.

Chapter 2 develops a conceptual framework relating the processes of individual movements and population dynamics to the spatial and temporal dimensions of temperature change. I find that most studies do not consider the dimensionality of temperature change when quantifying assemblage dynamics.

Chapter 3 finds that, on average, the abundance of reef fish species across their thermal ranges supports the 'abundant-niche centre' hypothesis. I also find a systematic pattern in the skew of realised thermal niches amongst species, which relates to latitude and biogeographic habitat variation.

Chapter 4 quantifies spatial patterns in the diversity of species' responses to heatwave events in five functional groups of reef fishes on the Great Barrier Reef and western Coral Sea. Browsing herbivores, scraping herbivores and corallivores have spatially homogenous patterns of response diversity indicating resilience at a regional scale. Further, all functional groups positively respond to temperature warming but only corallivores and excavators negatively respond to coral loss, and no functional groups strongly respond to algae loss.

Chapter 5 critically examines the 'wide-ranged winners' paradigm for terrestrial ectotherms (insects) across land-use types that represent a microclimatic gradient. I find that species' niche metrics consistently outperform geographic range size in predicting species occurrence. Species with warmer and drier affinities increased in occupancy in agricultural land uses which matched the expected warmer and dryer conditions.

Overall, realised niches are structured by abundance, exhibit diversity within local assemblages and regional species pools, and can predict occupancy at local scales even in thermally heterogeneous terrestrial systems. This thesis therefore further establishes the thermal niche as a core concept to quantify the dynamics of assemblages in a warming world. Chapter 6 critically evaluates the benefits and limitations of this niche perspective for quantifying biodiversity change and suggests future research avenues.

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Figure 5.4 Fitted relationship for trait-environment interactions for each case study Panel colours show each case study. X^2 values with 1-degree of freedom. *p*-values indicate significance of trait-environment interaction terms. Effects shown are marginal effects when all other geographic range and niche metrics are held at their mean values. Shaded regions are 95% confidence intervals. Note that non-significant terms are not shown including whole case-studies with no significant trait-environment interactions.

Figure 6.1 Factors that influence how well species' fundamental niches represent species' realised niches via species' distributions, and the consequences for predicting biodiversity change. The predictability largely depends on whether species distributions are in equilibrium with the environment and can maintain this equilibrium, and thus whether realised niches match fundamental niches. The capacity to track environmental change often determines this equilibrium (i.e., dispersal capacity, dispersal barriers). This predictability is linked to two methodological and conceptual frameworks which both centre around the species niche, as discussed in the main text. Example ectotherm taxonomic groups are placed along this spectrum, as well as the key taxonomic groups of focus in this thesis as represented by symbols in the top panel.

Research Thesis: Declaration of Authorship

Print name:	Conor Alexander Waldock
Title of thesis:	Ecological Assemblages in a Warming Climate: Addressing Knowledge Gaps in the Role of Thermal Heterogeneity and Realised Niches at a Global Scale

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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Waldock, C., Dornelas, M. & Bates, A.E. (2018) Temperature-Driven Biodiversity Change: Disentangling Space and Time. BioScience, 68, 873–884. doi: 10.1093/biosci/biy096

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Signature:	C.Waldock	Date:	23/04/2019

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Chapter 1 Introduction

1.1 Anthropogenic biodiversity change

> *'Of the many problems confronting society, surely one of the gravest is the likelihood that modern human culture may so change the intricate workings of the earth's ecosystems that they will no longer be able to provide the support that human culture requires for its existence.'* – Maurer, 1999.

The impact of human activities on ecological systems has a long history (Ellis *et al.*, 2013; Loughlin *et al.*, 2018). Current rates of agricultural expansion and land-use change (Newbold *et al.*, 2015), Anthropogenic climatic change (Warren *et al.*, 2018), and overexploitation (Jackson *et al.*, 2001; Lyons *et al.*, 2004) suggest human actions will affect the dynamics of species' populations, communities and ecosystems for centuries to come (Pereira *et al.*, 2010). Biological variation supports the resources that humans acquire from natural ecosystems (Cardinale *et al.*, 2012), therefore, there is an urgent need to understand the sources generating and altering this biological variation.

The term 'biodiversity' encompasses the variety of all life and the interactions amongst them - from genomes to biomes. In this thesis, I refer to 'biodiversity' as the variation in species' occurrence, abundance or identity within local assemblages (see Chapter 2, Box 1 for further discussion; Fauth *et al.* 1996; Magurran & McGill 2011). At this local assemblage scale, a recurring feature of Anthropogenic biodiversity change is the altered identity of species (assemblage composition) but not *necessarily* the loss in number of species (richness) found locally (Dornelas *et al.*, 2014, 2019; Gotelli *et al.*, 2017). While richness loss is often detected in assemblages – particularly when primary habitats are converted to agriculture – the decline in absolute number of species locally is often less pervasive than the turnover of species identities (Newbold *et al.*, 2015, 2016). Climate change, an emerging stressor on assemblages, can also result in little or no change in richness as communities both gain and lose species (Murphy & Romanuk, 2014). In Chapter 2, I review in detail the spatial and temporal structure of temperature change affects the gains and losses of species' populations causing assemblage reorganisation[1].

The differences in the species composition between local communities (i.e., beta-diversity) has declined too, as a result of biased assemblage turnover (i.e., the same

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[1] Therefore, I do not provide a full literature review of climate change effects on assemblages here.

species benefit across multiple locations). The causes of spatial beta-diversity declines include: the net persistent loss of local species richness (Baiser *et al.*, 2012); the increasing number of the same non-native species in local assemblages (McKinney & Lockwood, 1999); the increased abundance of the same native species in depauperate local communities after a disturbance (Tabarelli *et al.*, 2012; McCune & Vellend, 2013); and, the expanding ranges of 'winners' between many local assemblages (Savage & Vellend, 2014; Magurran *et al.*, 2015; Batt *et al.*, 2017). The increasing average range size in local assemblages is a further indicator of homogenisation as smaller-ranged endemics are lost and wider-ranged generalists colonise multiple sites (Batt *et al.*, 2017; Newbold *et al.*, 2018).

1.2 The promise and limits of a trait perspective of biodiversity change

> '*Contingency becomes overwhelmingly complicated at intermediate scales, characteristic of community ecology, where there are a large number of case histories, and very little other than weak, fuzzy generalisations.'* – Lawton, 1999.

Species traits can help predict assemblage responses to environmental change. Since the early 1990s a 'trait-based' approach to biodiversity change has been applied in many taxonomic groups, a broad set of stressors, and multiple environments (Figure 1.1; e.g., insects, De Palma *et al.* 2015; Aguirre-Gutiérrez *et al.* 2016; plants, Enright *et al.* 2014; fish, Richardson *et al.* 2018). For example, bird assemblage responses are mediated by species' traits where species with low clutch size and dispersal capacity have higher sensitivity to rainforest degradation (Pavlacky *et al.*, 2015). In general, changes in richness and trait-diversity metrics are incongruent because environmental filtering alters an assemblage's trait combinations, but not necessarily species richness (e.g., Strecker *et al.* 2011; De Palma *et al.* 2017). However, there are weaknesses in this trait-based argument that can be addressed through a niche-based perspective of biodiversity change: addressing gaps in this niche-perspective forms the empirical chapters of this thesis.

The central goal of a trait-based approach to biodiversity change is to provide more predictive and general insights (Figure 1.2; Webb *et al.* 2010, Mouillot *et al.* 2013, Enquist *et al.* 2015, Laughlin & Messier 2015). Species' traits evolve, in part, as adaptations to abiotic and biotic environments. As environmental conditions change from the conditions species traits are adapted to, fitness is expected to decline. Such response traits therefore provide a mechanism to explain species' changing presence in assemblages

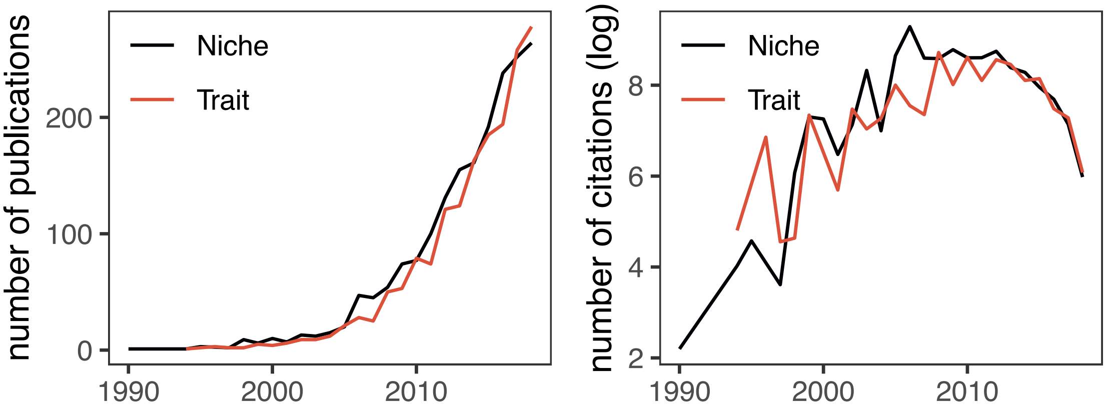

Figure 1.1 Niche- and trait-based approaches to understanding biodiversity change: (a) trends in number of publications and (b) the influence of these publications on biodiversity change research (mean no. citations) through time. Web of Science search for (niche) AND (biodiversity change), (trait) AND (biodiversity change) in the topics of ‘ecology’ and ‘biodiversity conservation’ up to 2019. Note the field initiation in the 1990s, a later exponential rise in the number of publications, and early highly influential papers in both topics (some overlap is likely).

exposed to environmental change (Kraft *et al.*, 2014). As such, variation in species' response traits within local assemblages is expected to predict, in part, responses to environmental change (Elmqvist *et al.*, 2003; Díaz *et al.*, 2013; Salguero-Gómez *et al.*, 2018). Response traits of species' assemblages are expected to simplify the myriad of context dependencies that govern a given species relative fitness within an assemblage (Lawton, 1999; Mcgill *et al.*, 2006; Agrawal *et al.*, 2007; Kraft *et al.*, 2014). Species can be grouped by their response traits to reduce assemblages to a simpler set of entities; or, be aligned along a spectrum of trait-variation (Díaz *et al.*, 2016). These response groups are expected to respond in a similar way to environmental change.

The trait-approach outlined above suffers a number of limitations. A single trait often inadequately describe species-environment relationships and therefore focal response traits may poorly represent a mechanism of species response (Statzner & Bêche 2010; Verberk *et al.* 2013; also see Thompson & Davis 2011 for invasion ecology perspecitve). For example, equal environmental fitness, and similar environmental responses, between individuals of two species can be achieved by completely different trait combinations (Figure 1.2b; Díaz *et al.*, 2013; Verberk *et al.* 2013). Trait-based approaches can lead to less general insights as a result of such context-dependencies between traits (Mlambo, 2014; Bartomeus *et al.*, 2018). In addition, higher taxonomic groups (e.g., Order, Class, Phylum) rarely share traits such as morphology and life-history stages. As such, a predictable relationship between traits and environments in one lineage is not widely applicable to others (but see Enquist *et al.* 2015). Insights from trait-based approaches then become siloed by taxa (Bruelheide *et al.* 2018, Wong *et al.* 2018, but see Cooke *et al.* 2019). Within a taxonomic group, or single assemblage, trait-based insights can be extremely informative (Mouillot *et al.* 2013; but see Bartomeus *et al.* 2018) but synthesising beyond single taxonomic groups becomes impossible. Once again, community ecologist are left with a set of special cases and idiosyncratic rules (Lawton, 1999; Vellend, 2010). These issues cannot be solved through better statistical tools (e.g., Webb *et al.* 2010) but relate to the conceptual basis of trait-based ecology (Verberk *et al.*, 2013). As a result, it is often difficult to leverage the proposed benefits of trait-based ecology against the question of biodiversity change (Figure 1.2; Mcgill *et al.* 2006, Webb *et al.* 2010).

Having addressed some pitfalls in trait-based investigations of biodiversity change it is useful to ask then, what are the benchmarks of a general and predictive framework to study biodiversity change? I would argue that any framework proposing to general and predictive and should provide:

i) a quantitative prediction of changes to local assemblage composition with a given change in an environment;

ii) changes to assemblages estimated at an individual, population or species level which provides a mechanism for assemblage compositional changes (i.e., an understanding of **how** the comprising parts of an assemblage respond);

iii) a comparable underlying mechanism explaining individual, population or species responses between taxonomic groups, regions and realms (i.e., an understanding of **why** the comprising parts of an assemblage respond in particular way);

iv) a 'whole' assemblage perspective such that all responses at the focal scale can be examined by identical methodologies (i.e., mechanisms are measured in the same way).

Focusing on environmental niches rather than traits may offer a simple organising principle to gain more general and predictive insights to changes in species' assemblages with environmental change. Chapters 3-5 aim to address knowledge gaps in the aspects of niche theory that are relevant for understanding biodiversity change, as outlined below.

1.3 A niche perspective of biodiversity change

> *'The total environment of a species, a population, or an individual is thus examined through its 'biological eyes', and its observed biological response is a function of what it 'sees''* – Maguire, 1973.

1.3.1 Defining 'the niche'

The niche concept has been quantified and used in many ways (Peterson *et al.*, 2011; McInerny & Etienne, 2012b) with a long history of multiplicity (Grinnell, 1917; Hutchinson, 1957). Throughout this thesis, I limit my consideration of the niche as individual's and species' response to the abiotic environment (although other niches are available see Figure 1.3; McInerny & Etienne, 2012b). The niche concept is applicable at individual and species scale depending on if intraspecific variation is important to consider, I mainly consider the species scale in this thesis.

A niche can be conceptualised as the abiotic environment conditions where individuals' fitness results in a positive instantaneous population growth rate (Figure 1.3; Holt, 2009;

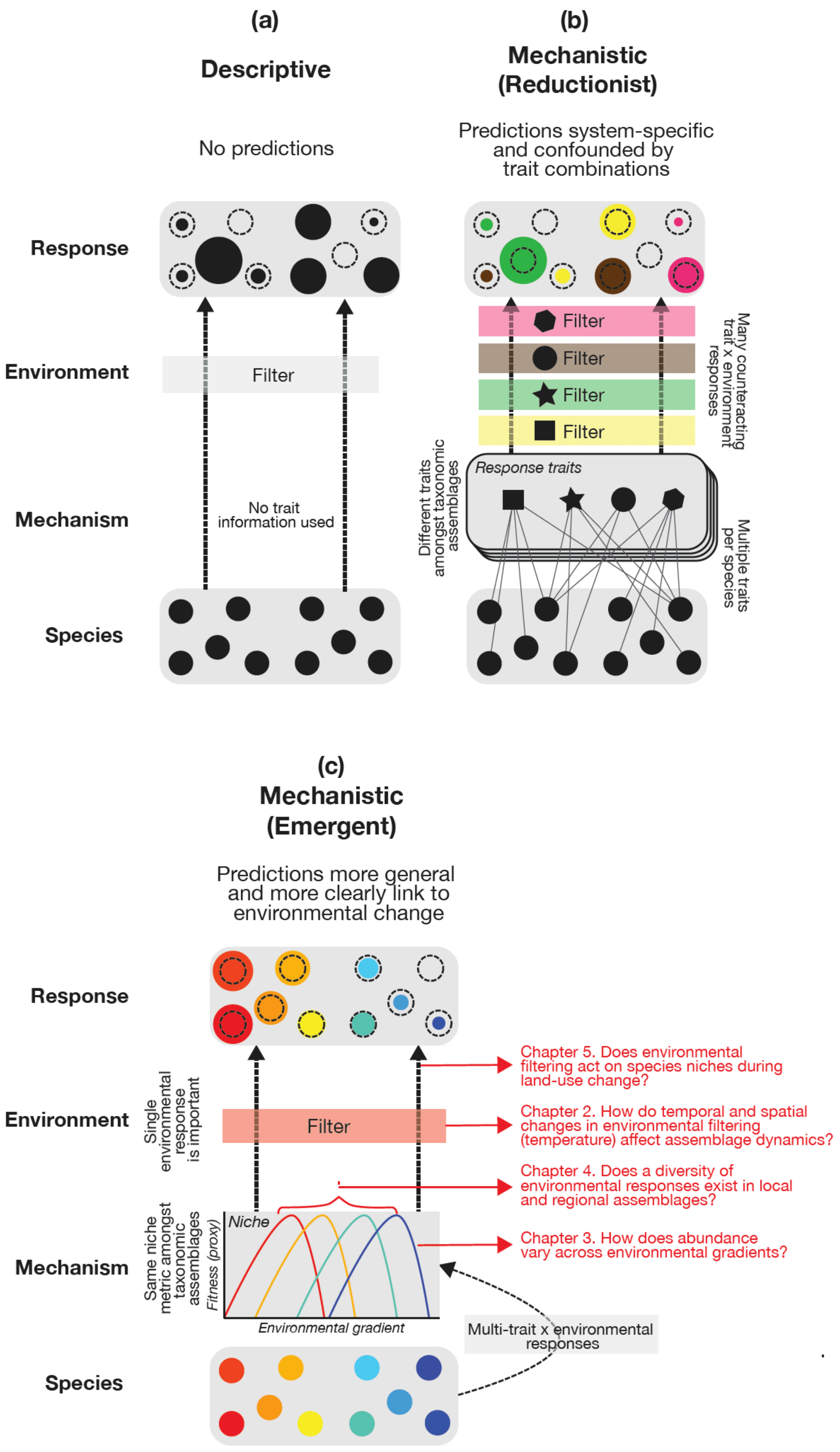
(a)
Descriptive
No predictions
(b)
Mechanistic (Reductionist)
Predictions system-specific and confounded by trait combinations
Response
Environment
Mechanism
Species
Filter
No trait information used
Filter
Filter
Filter
Filter
Many counteracting trait x environment responses
Response traits
Different traits amongst taxonomic assemblages
Multiple traits per species
(c)
Mechanistic (Emergent)
Predictions more general and more clearly link to environmental change
Response
Environment
Mechanism
Species
Single environmental response is important
Filter
Same niche metric amongst taxonomic assemblages
Niche
Fitness (proxy)
Environmental gradient
Multi-trait x environmental responses
Chapter 5. Does environmental filtering act on species niches during land-use change?
Chapter 2. How do temporal and spatial changes in environmental filtering (temperature) affect assemblage dynamics?
Chapter 4. Does a diversity of environmental responses exist in local and regional assemblages?
Chapter 3. How does abundance vary across environmental gradients?

Figure 1.2 Schematic of taxonomic (a), functional trait (b) and niche (c) perspectives on quantifying and predicting assemblage responses to environmental change. Species are filtered based on their traits which interact with different aspects of environmental change, because natural selection acts on multiple traits at once, and many trait combinations exist that lead to equal fitness, the outcome of species responses can be unpredictable (a and b redrawn from Verberk et al. 2013). Furthermore, traits vary amongst taxa leading to less generalisable insights (stacked traits in b). The niche approach (c) quantifies fitness variation across environmental gradients to predict responses to environmental change. Using a niche approach 'skips' over understanding each response trait's effect for each environmental factor. Instead, a niche approach looks at the overall fitness responses of species across environmental gradients. In red are the questions addressed by the chapters in this thesis.

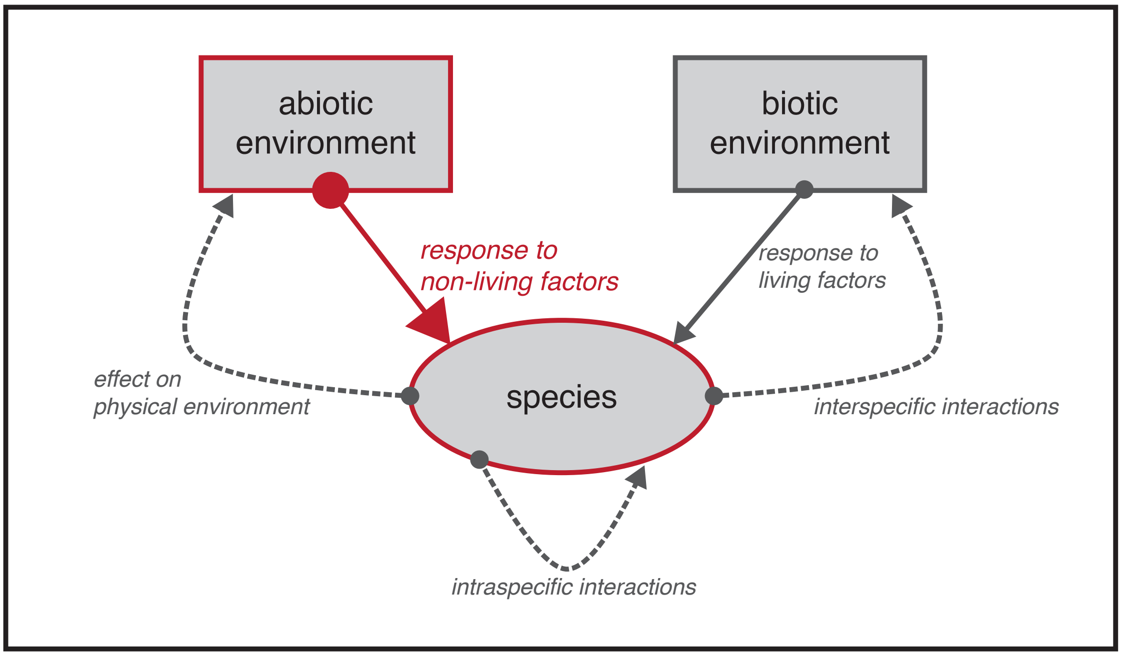

Figure 1.3 The linkages between niche concepts presented in McInerny & Etienne, (2012b). The focal niche relationship discussed throughout this thesis is shown in red. Response niches are with solid arrows and represent species responses to abiotic or biotic environments, effect niches are in dashed lines and describe the role of a species in how it effects the environment. Redrawn from Figure 2 in McInerny & Etienne (2012b).

Pironon *et al.*, 2017). The parallel between trait- and niche-perspectives of biodiversity change is clear: the niche is the emergent property of how multiple traits interact with an environment to determine the fitness of an individual, or relative fitness of a species (Figure 1.2c; Violle & Jiang, 2009; Laughlin & Messier, 2015). Therefore, explaining why certain species in an assemblage prosper with environmental change, does not require identifying the mechanism by which traits confer fitness (as suggested by trait-based approaches; Kearney et al. 2010; Laughlin and Messier 2015; Figure 1.2c). Instead, we must only identify how fitness, or a proxy thereof, varies across an environment for a given individual or species. For a local assemblage, each species' relative fitness responses to an environmental change provides a mechanism helping to explain assemblage change (where mechanism here is defined as 'the processes responsible for some natural phenomenon'; McGill & Potochnik 2018). Using species niches is therefore more general than trait-based approaches, and may still be predictive. This is a macroecological perspective because we use an emergent property (species niche) as a whole, rather than a more reductive approach of defining each trait-by-environmental response, to understand biodiversity change (Figure 1.2, McGill 2019).

1.3.2 Niches and biodiversity change

Two classes of niches help quantify the change in performance of species within assemblages during environmental change, often separated by their methodological approach (i.e., ostensive definitions of the niche, McInerny & Etienne 2012a). Forward approaches derive relationships between proxies of fitness (such as energy balance, demographic rates, or population growth rates) and environments using experiments, or by mechanistic modelling based on first principles (Holt, 2009; Kearney *et al.*, 2010). Applying a forward approach to an assemblage is limited by the logistic challenge in quantifying relationships between fitness and environmental variation for multiple species (Kearney & Porter, 2009; Mokany & Ferrier, 2011). At present, quantifying environment-performance curves mechanistically for whole assemblages (i.e., criteria 'iv' above) is limited to small organisms in systems that can be more easily controlled and replicated (but see Guy-Haim, 2017). Notably, Garcia et al. (2018) quantified the thermal response of bacterial species' growth rate experimentally, and found that niches explain changing relationships between biodiversity and ecosystem functioning with warming.

Backward niche approaches (McInerny & Etienne, 2012a) define species environmental niche from species observed distributions in environmental space; using properties of that distribution to predict assemblage change. This niche measure is referred to as a realised niche, because it represents the geographic realisation of a species' fundamental niche (Hutchinson, 1957). Using realised niches assumes populations have positive growth rates when present in an environment. The availability of species occurrence data (i.e., www.gbif.org; Meyer *et al.* 2015) and development and proliferation of modelling tools such as species distribution models (SDMs), and multi-species versions of SDMs, has made the realised niche approach popular to quantify assemblage dynamics at large spatial scales (Ferrier & Guisan 2006, Bellard *et al.* 2012, Mokany *et al.* 2012; although this thesis is not specifically tied to SDM approaches). Often, there is a focus on the thermal dimension of a species' realised niches because of the availability of temperature data (e.g., Fick & Hijmans 2017); the availability of spatial projections of climate change (van Vuuren *et al.* 2011); and, the societal importance of understanding the effects of climate-change on biodiversity (Hoegh-Guldberg *et al.*, 2018). This thesis mostly focuses on temperature, and thermal niches, which is well justified in marine ecosystems and for ectotherms (Beaugrand *et al.*, 2013; Beaugrand, 2014a; Payne *et al.*, 2016) this limitation is discussed in Chapter 6. In Chapter 5, I test if thermal niches are also important on land, where species' distributions are more constrained by local factors (Sunday *et al.*, 2012, 2014).

Species thermal realised niche is often recognised as a powerful approach to quantify assemblage dynamics in response to environmental warming (Ferrier & Guisan, 2006). Indeed, the grandiose 'Macroecological Theory of All Life' (METAL; Beaugrand, 2014b) suggests that species niches, largely alone, provide a key mechanism underpinning assemblage compositional shifts and ecosystem change (Beaugrand, 2014b; Beaugrand *et al.*, 2019). METAL theory posits that niche structure, variation in niche optima, and variation in niche shape interact with warming to drive assemblage turnover and compositional shifts (Beaugrand, 2014b). Indeed, using METAL theory Beaugrand et al. (2019) showed that dramatic shifts in community composition through time can be predicted based only on thermal niches and temperature change for 14 pelagic plankton assemblages. Observational studies confirm that species niches can underpin assemblage dynamics with warming (see Chapter 2 for further details). For example, in shallow-water rocky-reef assemblages, warming caused an increase in species with warmer realised thermal niches during both shorter-term warming events (Wernberg *et al.*, 2016; Day *et al.*, 2018) and over longer periods of warming (Bates *et al.*, 2014a; Horta e Costa *et al.*, 2014; Bates *et al.*, 2017). In addition, the average thermal affinity of birds and butterflies has tracked climate warming over the last 20 years in Europe (Devictor *et al.*, 2012); also, birds with warm-affinity thermal realised niches have increased in abundance in the USA (Stephens *et al.*, 2016).

1.3.3 Considering abundance in thermal niches

Most studies quantify species' realised niches by inferring fitness from presence or absence at sites. Andrewartha and Birch (1954) noted that the '…distribution and abundance are but the obverse and reverse aspects of the same problem'; as such, other than data constraints, a focus on occurrence (distributions) is unwarranted. Species distribution models typify the use of occurrence data to define realised niches (Austin, 2007; D'Amen *et al.*, 2015; Ashcroft *et al.*, 2017). Distribution modelling approaches that do consider abundance often require rich demographic data for a given species, which limits the applicability across assemblages (Pagel & Schurr, 2012; Renwick *et al.*, 2012). The first step to quantifying realised thermal niches from abundance data is documenting patterns of abundance across species' geographic ranges and environmental gradients, which has a long history (e.g., Andrewartha & Birch 1954; Brown, 1984). However, the distribution of abundance does not appear to conform to a predictable structure across species ranges or environmental niches (Sagarin *et al.*, 2006; Pironon *et al.*, 2016; Dallas *et al.*, 2017; Santini *et al.*, 2018). Data quality constraints may have some role to play in the difficulty in detecting patterns in the distribution of abundance (Knouft, 2018; Santini *et al.*, 2018) because abundance data are less frequently available than occurrence data and are rarely collected in a standardised was between different locations (but see Sauer *et al.* 2013). The environmental distribution of species' abundance is therefore an important knowledge gap when applying realised niche theory to better understand assemblage dynamics. I attempt to narrow this gap in Chapter 3 by quantifying abundance variation across thermal gradients – I infer this as a measure of species realised thermal niches – for hundreds of shallow-water reef fishes using exemplary standardised data. Thus, I quantify species' responses to environmental gradients in Figure 1.2c.

Abundance information can inform management and refine understanding of biodiversity change. For example, population abundance is recognised as a strong correlate of extinction risk (O'Grady *et al.*, 2004) and a precursor to range area decline (Gaston *et al.*, 2000) and range shifts (Bates *et al.*, 2014b; Lenoir & Svenning, 2015). Abundance is used to help designate the conservation status of populations (IUCN, 2000; Santini *et al.*, 2019) and indicate biodiversity change in managed (Edgar *et al.*, 2014; Geldmann *et al.*, 2018) and unmanaged systems (Collen *et al.*, 2009). Further, abundance contributes to compositional shifts in assemblages (Davey *et al.*, 2012) as well as assemblage contributions to ecosystem functioning (Winfree *et al.*, 2015).

1.3.4 Considering diversity in thermal niches

Within a local assemblage, species often vary in their thermal niches which can lead to idiosyncratic responses amongst species (Day *et al.*, 2018; Flanagan *et al.*, 2018; Garcia *et al.*, 2018; Selden *et al.*, 2018). Diversity in species' thermal niches influences overall compositional turnover, such that an assemblage-level response to temperature change are not necessarily linear (Figure 1.4; Blonder *et al.*, 2017; Flanagan *et al.*, 2018; Gaüzère *et al.*, 2018). For example, the 'community temperature index' (CTI) measures the species' thermal affinity (average temperature across a species range) averaged across all species in a local assemblage. CTI is a common metric to measure how climate change affects local assemblages; signalling the direction of climate-driven compositional reorganisation of communities. However, the observed change in local assemblage CTI depends the regional diversity of thermal niches (Figure 1.4; Flanagan et al. 2018). This thermal diversity is important to better understand the provisioning of ecosystem functions in warmer more variable environments (Dee *et al.*, 2016; Garcia *et al.*, 2018; Selden *et al.*, 2018). Furthermore, a diversity of thermal responses to climate change providing a form of resilience to assemblages, whereby changes to the ecosystem functions provided by assemblages are slower than the rate of climate change (Elmqvist *et al.*, 2003; Kühsel & Blüthgen, 2015). However, linking thermal niche diversity to ecosystem functioning is often limited methodologically: using proxies of thermal niche diversity (Dee *et al.*, 2016); examining a limited number of species (Selden *et al.*, 2018), or limited to highly constrained experimental systems (Garcia *et al.*, 2018). Overall, estimating how thermal niche diversity in whole assemblages influences biodiversity and ecosystem functioning with warming is a general knowledge gap that I address in Chapter 4.

1.3.5 Are thermal niches relevant to terrestrial drivers of biodiversity change?

On land, temperature exhibits two to three times more spatial and temporal variability than in the oceans (Steele, 1985; Steele *et al.*, 2018). The heterogeneity of temperature on land might influence how well realised niches relate to assemblage change. For example, terrestrial organisms take advantage of local-scale heterogeneity and buffer assemblage responses to broad scale environmental change (De Frenne *et al.*, 2013). As such, niches described from coarse-scale occurrence and environmental data might poorly represent the environment experienced by terrestrial organisms (Sunday *et al.*, 2014; Pincebourde *et al.*, 2016). Therefore, coarse-scale thermal niches may poorly predict assemblage responses to environmental change. I test if realised niches predict biodiversity change on land by studying the effect of microclimatic shifts caused by

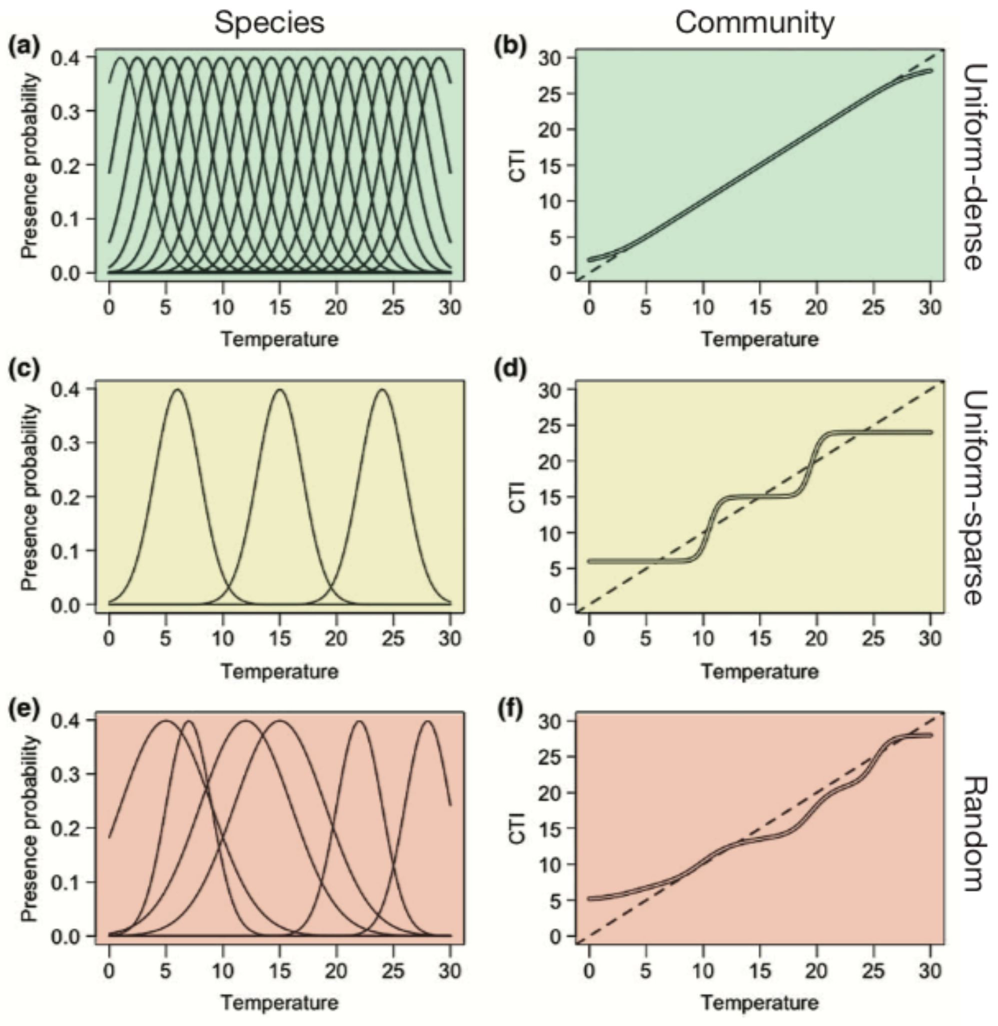

Figure 1.4 The change in composition of a species' assemblage depends on the distribution, diversity and shape of species' thermal niches, from Flanagan *et al.* (2018). Thermal niche variation at the species level manifests as different expected rates of change in community composition, indicated by community temperature index (CTI), relative to a change in temperature at the community level. (a) When species thermal niches are uniformly and densely packed a 1:1 relationship between local temperature and CTI is expected (b), this relationship changes if species are sparely packed (c) leading to a step change in CTI as the dominant species turnover (d). In reality, communities may be assembled from broad and narrow niche species (e) such that community composition shows variable changes than depend on assemblage thermal niche diversity (f).

land-use change. Converting mature forests to agriculture causes local habitats to be on average warmer, more variable, and drier (Senior *et al.*, 2017; De Frenne *et al.*, 2019). Species with wider geographic ranges often benefit from land-use change (Scott *et al.*, 2006; Newbold *et al.*, 2018) and it is implicitly assumed that the functional traits that result in broader geographic ranges also enable species to colonise novel environments, or cope with disturbance. However, environmental tolerance limits and breadth (e.g., environmental limits to survival or reproduction) are also strong determinants of geographic range size (Slayter *et al.*, 2013; Kambach *et al.*, 2019) and the capacity to cope with land-use change (Nowakowski *et al.*, 2018b). Whether environmental niches predict species responses to land-use change beyond the effect of the traits that drive larger species geographic ranges remains an important knowledge gap. Land-use change is one of the most important factors affecting biodiversity at present (Maxwell *et al.*, 2016) and will remain important in the future (Pereira *et al.*, 2010) largely due to agricultural expansion and intensification – the general relevance of a niche-approach is important to test. Finally, examining the influence of niches during land-use change rarely occurs at an assemblage scale (e.g., Frishkoff et al. 2015, Nowakowski et al. 2018) but developing assemblage-scale frameworks is important (Pincebourde *et al.*, 2016; Tuff *et al.*, 2016; Nowakowski *et al.*, 2018a).

1.4 Thesis overview

The availability of data on the distribution of biodiversity is greater than ever before through coordinated efforts to synthesise biodiversity information (Edwards, 2000; Graham *et al.*, 2004; Soberón & Peterson, 2004). However, biodiversity data has limitations in being taxonomically biased and opportunistically collected, which leads to spatial and temporal patchiness (Ballesteros-Mejia *et al.*, 2013; Beck *et al.*, 2014; Meyer *et al.*, 2015). Inferences of biodiversity change are therefore biased (Gonzalez *et al.*, 2016). Yet, imperfect data can still be useful. Better strategies to efficiently use the current information available are necessary to build the theory and knowledge to underpin effective conservation decisions. The last few decades of research (Figure 1.1) has revealed that a niche-based perspective, often based on limited distribution data, offers many avenues forward. An overarching aim of this thesis is to use available distribution data to better quantify and use species realised environmental niches, set in the context of identifying mechanisms of assemblage-scale biodiversity change.

In Chapter 2, I provide a literature review of how spatial and temporal dimensions of temperature change underpin assemblage dynamics (Chapter 2; Garcia et al. 2014). I develop a conceptual framework to link temperature to biodiversity change. This framework explicitly considers temporal and spatial dimensions of temperature change, thus moving the focus away from assemblage responses to mean temperature change. Doing so highlights a central role of species' niches in assemblage dynamics. I next explore knowledge gaps surrounding the application of realised niches to assemblage dynamics.

In Chapter 3, I quantify the structure of abundance across thermal distributions in shallow-water reef fish, I therefore estimate species realised thermal niche shapes from abundance data. I use the citizen-science project 'Reef Life Survey' (RLS, Edgar & Stuart-Smith, 2014) which provides exemplary standardised surveys for hundreds of species across thousands of locations. This data therefore provides unique insights to the distribution of abundance across species' thermal ranges. I find that species were in general most abundant at the centre of their realised thermal niche, however, abundances are sometimes skewed towards thermal niche edges. Thus, a diversity of thermal niche shapes, defined by abundance responses to temperature gradients, exists in regional species pools.

In Chapter 4, I use RLS data to further investigate the diversity in realised thermal niches (and other niche axes relevant to heatwave events). I examine niche response diversity of local reef-fish assemblages and regional species pools. I focus on species that modify benthic habitats by feeding on coral and algae which are expected to affect the resilience of coral reefs to climate change. I first aimed to investigate spatial patterns in response diversity. Second, I aimed to test, through simulations, which functional groups are sensitive to which particular components of heatwave events that normally co-occur simultaneously (e.g., warming, shifts in coral and algae cover). Using a novel response diversity framework, I present a holistic view of niche response diversity, using standardised metrics amongst functional groups for a whole regional species pool.

In Chapter 5, I examine how realised niches affect the occurrences of species in local assemblages in more thermally heterogeneous terrestrial systems across environmental gradients induced by land-use change. Here, I use the 'Projecting Responses of Ecological Diversity In Changing Terrestrial Systems' database to study occupancy responses to land-use change (PREDICTS, Hudson et al. 2014, 2017). I estimate species realised niches using data from the Global Biodiversity Information Facility (GBIF, www.gbif.org). I find that realised niches predict the effect of land-use change on local species' occurrence, but the effects of different realised niche axes were context-dependent. I demonstrate that realised niches can be a simple to quantify and widely applicable tool to help predict biodiversity responses to (microclimatic) warming even in heterogeneous terrestrial systems.

In Chapter 6, I synthesise the results of this thesis in the context of assemblage compositional change; presented as a key response of local assemblages to Anthropogenic environmental change. I discuss the relative importance of temperature as a predictor of occurrence and abundance across ecological systems: outlining limitations in the utility of realised niches to understand assemblage dynamics. I also examine how organismal, spatial and temporal scales of realised niches can influence predictions of biodiversity change. I outline how the results of this thesis are relevant for environmental management in a warming world.

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Chapter 2 Temperature-driven biodiversity change: disentangling space and time

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2.1 Abstract

Temperature regimes have multiple spatial and temporal dimensions that have different impacts on biodiversity. Signatures of warming across these dimensions may contribute uniquely to the large-scale species redistributions and abundance changes that underpin community dynamics. A comprehensive review of the literature reveals that 86% of studies were focused on community responses to temperature aggregated over spatial or temporal dimensions (e.g., mean, median, or extremes). Therefore, the effects of temperature variation in space and time on biodiversity remain generally unquantified. In the present chapter, I argue that this focus on aggregated temperature measures may limit advancing our understanding of how communities are being altered by climate change. In light of this, I map the cause-and-effect pathways between the different dimensions of temperature change and communities in space and time. A broadened focus, shifted toward a multidimensional perspective of temperature, will allow better interpretation and prediction of biodiversity change and more robust management and conservation strategies.

2.2 Introduction

Environmental temperature is a primary variable important for biological function at all organisational scales. Even slight temperature changes can dramatically affect biological processes from cells to populations, with strong ecological consequences. At the smallest scale, temperature drives cellular reaction rates through kinetic processes. Individuals respond directly to environmental temperature – for example, by modulating their activity rates (Payne *et al.*, 2016, 2018). Population demographic rates are also temperature sensitive (Dell *et al.*, 2011), with consequences for abundance and occupancy patterns. Demographic changes in combination with individual effects (e.g., foraging velocity, ingestion rates; Dell *et al.* 2011) lead to shifts in species interaction strengths (disease prevalence, Kock *et al.* 2018; parasitism rate, Runjie *et al.* 1996), ultimately translating to change in community dynamics and structure (Kordas *et al.*, 2011; Bellard *et al.*, 2012).

Environmental temperature is highly variable in both space and time. Some aspects of environmental temperature are predictable (e.g., seasonal changes), others are not (e.g., extreme events). Therefore, a temperature regime has multiple dimensions that can be described in both space and time, with the potential to shape biological patterns in different ways (Garcia *et al.*, 2014). For example, as we move from the tropics to the poles, it becomes colder, daily variability decreases, but seasonal variability increases (Wang & Dillon, 2014). Distinct signatures of spatial variability also exist; for example, temperature is much more spatially heterogeneous in intertidal systems than in subtidal systems. Along these different axes of temperature dimensions in space and time, there is an additional layer of gradual long-term warming due to anthropogenic climate forcing (IPCC, 2013).

Climate change is altering environmental temperature regimes. The spatial arrangement (i.e., spatial heterogeneity) and timing of temperature change is typically abstracted to a statistical distribution, defined presently and by others as temperature magnitude (see box 1 and Garcia *et al.* 2014). However, by examining only temperature magnitude (e.g., its mean), we are deprived of the detailed dynamics of spatial and temporal temperature change. The position and availability dimensions of temperature change can vary, even without shifts in the overall mean temperature of a region or through time (see box 1 and Figure 2.1 for further definitions; Garcia *et al.* 2014). For example, the movement of thermal isoclines with warming is an example of a shift in the position of temperature in space (Loarie *et al.*, 2009; Burrows *et al.*, 2011; Hamann *et al.*, 2015). The earlier onset of spring represents a change in position of temperature in time (Wang & Dillon, 2014). Changes to the availability of temperature depend on physical area or temporal duration of particular temperature signatures within a region or time slice (Williams *et al.*, 2007; Ordonez & Williams, 2013).

In the present chapter, I identify the underlying spatial and temporal components (availability and position) overlooked by summary distributions (magnitude). For example, as isotherms shift away from a particular location, warming at the location may occur, but the spatial context of temperature change will influence the regional setting of biodiversity change. Changes to the spatial and temporal arrangement and location of temperatures can often be statistically independent of mean temperature changes and,

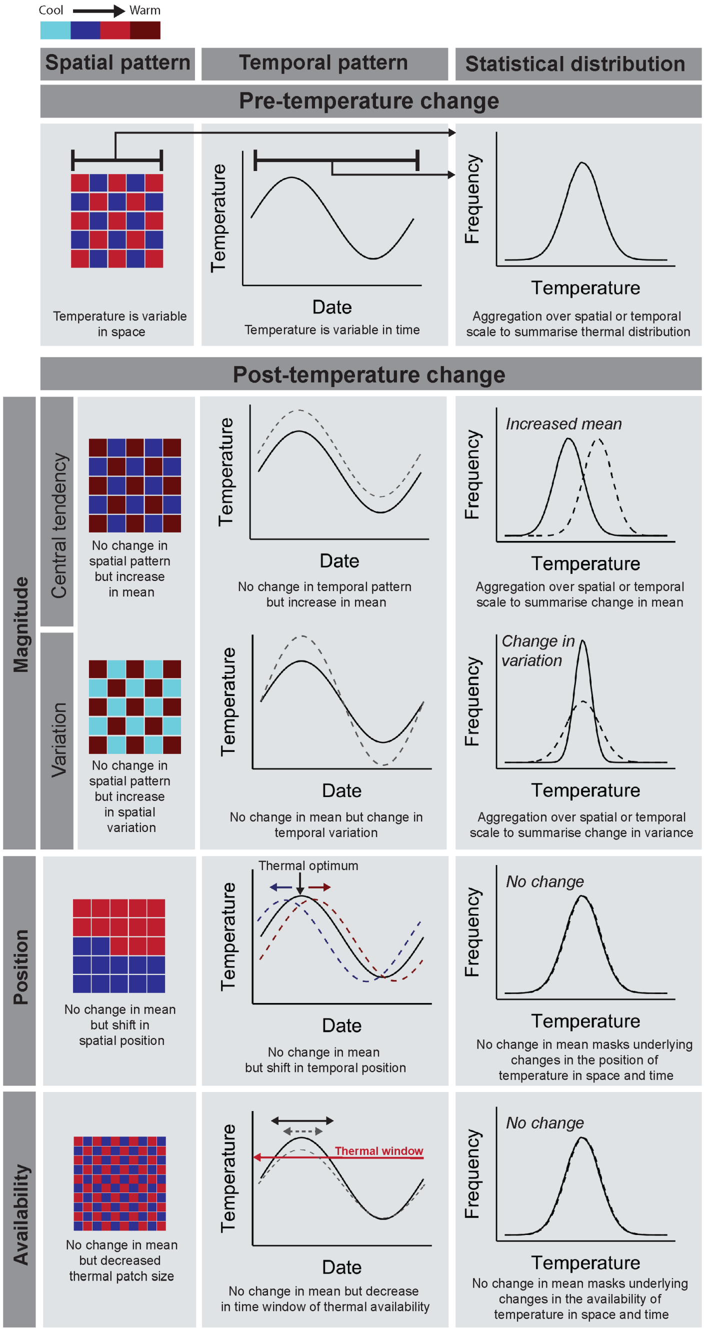

Figure 2.1 Temperature patterns in defined spatial and temporal units and their change through time. Temperature is variable in both space and time, but to aggregate to a mean value, a researcher must select scales of space and time to describe a particular statistical temperature distribution. Changes in a statistical distribution (e.g., central tendency and variation) can occur with no changes to the underlying spatial or temporal organisation of temperature within those defined units (e.g., 50 square kilometres, 1 year). Likewise, even if no change is observed in the statistical distribution, underlying shifts in space and time may be masked, in both availability and position of temperature. I outline a few, of many, possible scenarios by which temperature magnitude, position, and availability can change.

Box 2.1 Defining and measuring temperature and biodiversity change in space and time.

Temperature regimes – the characteristic pattern of temperature variation in space and time for a given scale – vary across the Earth. For example, temperate regions since the Late Quaternary have been characterised by cool and warm periods (i.e., seasonality) through the year and relative cool climates. Four different dimensions of a temperature regime are generally recognised (see Garcia *et al.* 2014), and how they vary with climate change is described in the present chapter (see Figure 2.1). Temperature magnitude describes the change in the statistical distribution of temperature for a given locality. The statistical distribution is defined by both its central tendency (e.g., changing mean – i.e., warming or cooling) and its dispersion (e.g., increasing variation, skew or kurtosis – i.e., extreme events). The rate of change in temperature magnitude is defined by the change in the statistical parameter (e.g., mean, standard deviation) per unit time.

Underlying this change in temperature magnitude are changes to temperature position and temperature availability in space and time (Figure 2.1). Temperature temporal position describes the change in the timing (i.e., date) of a specific temperature event within a defined spatial unit. This contrasts with temperature temporal availability, which describes a change in the total duration of a specific temperature event within a defined spatial unit. Temperature spatial position is defined by the relocation of temperature to a new area (i.e., isotherm shift change in linear distance) for a given temporal unit (Loarie *et al.* 2009, Hamann *et al.* 2015, Figure 2.3). In contrast, temperature spatial availability measures the change in area or size of a temperature available within a geographic location (i.e., the change in geographic space of a temperature regime measured in square kilometers, km2) for a given temporal unit (Figure 2.3). Novel climates are an important component of temperature spatial availability and describe the availability of new climatic space, increasing from an initial area of 0 km2 (Williams *et al.*, 2007).

Likewise, community metrics also fall into the following broad categories to measure structural and compositional differences in species assembled at local scales: species richness, total abundance, species relative abundance, compositional and trait based (Smith *et al.*, 2009; Magurran & McGill, 2011; Hill *et al.*, 2016; Santini *et al.*, 2017). These are important to recognise when matching the measured community responses to the processes driving change (i.e., section 2.5). The total number of different species in a community is measured using species richness metrics. The net loss and gain of species translates to a change in richness. The total abundance of a community is simply the sum of all individuals in a community and is often related to species richness as a result of sampling effects (i.e., more individuals increases the probability of a new species being present). The distribution of individuals between species represents the structure of a community and is often summarised by the shape of species relative abundance distributions. A change in structure occurs with shifts in species relative abundances (e.g., few rare species versus many common species), but these changes are agnostic to species identity (i.e., the same structure, but the assemblage comprises all new species). Therefore, structural change can represent richness and total abundance changes simultaneously. Compositional metrics describe how both species' relative abundances and identities shift and therefore measure the reorganisation of species abundances in a community. The losses or gains of species measures the turnover component of compositional change (Baselga & Leprieur, 2015). Finally, trait-based metrics quantify the diversity, range and values of the traits and niche properties of species within a community; these are often relevant to a particular driver of interest (e.g., species thermal limits and warming).

therefore, decoupled from mean temperature changes (Garcia *et al.*, 2014). Therefore, it is important to ask what we might miss by interpreting biodiversity responses to climate change exclusively as a summary of a statistical distribution and what can be gained by explicitly considering how temperature change manifests in space and time as availability and position change.

There is a further challenge in linking community-level change directly to the different dimensions of temperature change, because this requires disaggregation of a community into meaningful response units. Communities – groups of species that share environments at a given time and location with the potential for species to interact (Fauth *et al.*, 1996) – are complex biological units. As with temperature regimes, communities can also be characterised by many distinct dimensions (see box 1 for definitions). Examples of these dimensions include the number of species (species richness), the total number of individuals (abundance), the distribution of individuals among different species (relative abundance), the combined mass of all individuals (biomass, a measure of energetic consumption and productivity), and the variety of individuals and species (genetic and phylogenetic diversity) and their characteristics (functional diversity). Therefore, different aspects of biodiversity are affected by a suite of factors, leading to difficulty in identifying with confidence which factors are mechanistic drivers of emergent patterns (Lawton, 1999). As with considering changes in the temperature regime, the challenge becomes even greater when the additional complexity of community dynamics through time is of interest (McGill *et al.*, 2015). Certain community dimensions are responsive to environmental changes, such as the composition and relative abundance of assemblages (Hill *et al.* 2016), whereas others, such as species richness, are less directly responsive to environmental change (Santini *et al.* 2016), with increases or decreases being highly dependent on measurement scale (Vellend *et al.*, 2017). The multidimensional nature of both temperature and biodiversity variables justifies the aim of the present chapter: to map predictions of cause-and-effect among different dimensions.

2.3 Literature review

To determine what dimensions of temperature regime and community responses are most commonly studied, I reviewed articles published from 2005 until 2015 (see Appendix 1 for methods and detailed discussion). I found that, in spite of the complexity in changing temperature regime, most research has been focused on identifying responses to mean warming trends. Of the 156 papers returned from this literature review, 86% were focused on temperature magnitude, and only a small proportion of research has investigated spatial position (3%) and availability (1%) or temporal position (4%) and availability (6%, Figure 2.2). Of the metrics used to describe changes in temperature magnitude – the changing statistical distribution of temperature – mean changes were investigated in 48% of the studies, and 41% of the studies were focused on minimum or maximum temperatures. I also found a strong bias toward species richness (36%) rather than toward species identity (13%) or relative abundance (6%) as the predominant dimension of communities measured in responses to temperature change. Therefore, the spatial and temporal complexity underlying temperature change is rarely considered as a driver of community dynamics, instead temperature is generally abstracted over spatial or temporal scales to an aggregate mean value.

2.4 Objectives and purpose

Trends in the responses of biodiversity that have been detected and attributed to particular dimensions of temperature change in space and time are emerging. No-analogue communities have formed as species reshuffle in response to the development of novel temperature regimes (Urban *et al.*, 2012). Increases and decreases in species richness have been attributed to changing species distributions following locational shifts in thermal isoclines (Devictor *et al.*, 2012; Batt *et al.*, 2017). Changing temperature regimes have also been implicated in driving the increasing relative abundance of widespread and common species, or homogenisation, of communities (Davey *et al.*, 2012; Magurran *et al.*, 2015). There is widespread evidence of shifts toward species with thermal preferences for warmer environments (Bates *et al.*, 2014a; Horta e Costa *et al.*, 2014; Gaüzère *et al.*, 2015; Stephens *et al.*, 2016; Tayleur *et al.*, 2016), a process known as tropicalisation or thermophilisation.

Notwithstanding these few examples, how different dimensions of temperature change will affect the dynamics of multidimensional communities is poorly established at present. To address this gap, I developed a conceptual framework to guide predictions and explicit quantitative tests of biodiversity change in response to temperature change, measured in the appropriate dimensions of space and time (O’Connor *et al.*, 2015; Houlahan *et al.*, 2017). I further illustrate below why neglecting the dimensionality inherent to both temperature regime and biodiversity change may prevent accurate predictions. I focused on changes in the richness of local communities and homogenisation over space as illustrative examples of biodiversity change that are driven by multiple temperature change dimensions.

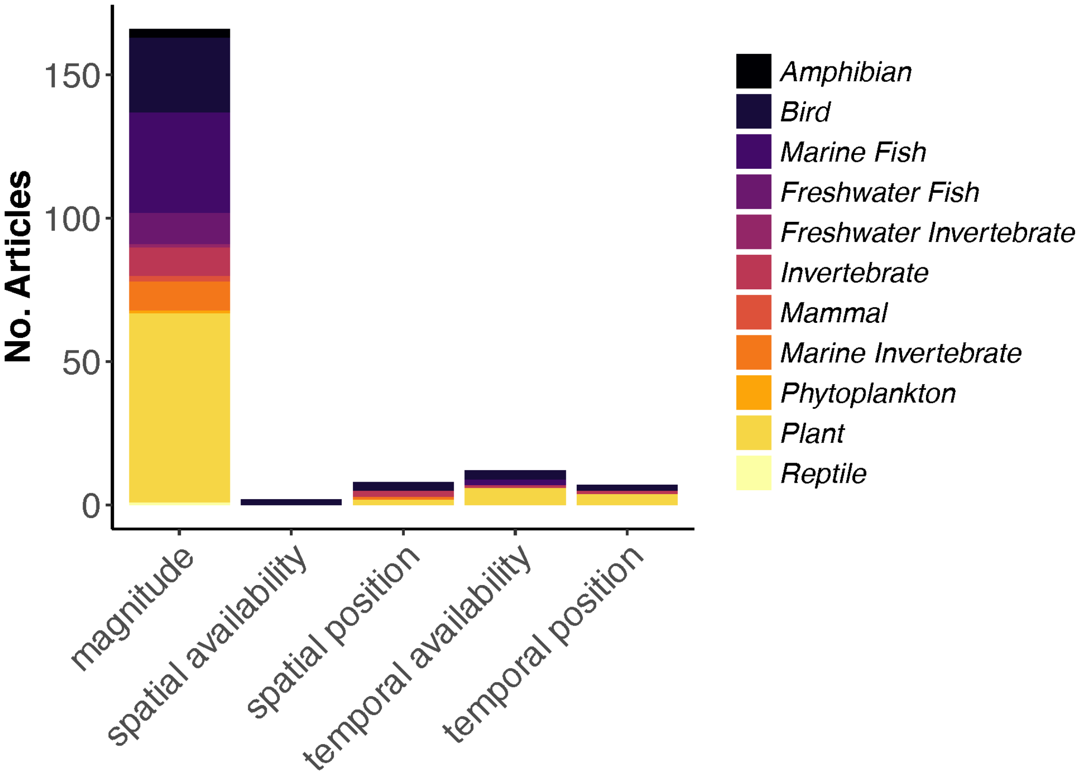

Figure 2.2 Magnitude of temperature change dominates our understanding of temperature change. The number of articles assessing community response to temperature change per dimension of temperature change representing 11 taxonomic groups from 2005 until 2015.

2.5 Linking community change processes and temperature dimensions

Two community processes are relevant to understand community dynamics at anthropogenic time scales – selection and movement (Vellend, 2010, 2016). The selection and movement of individuals lead to change in richness, structure, composition of communities, and traits of the species present. These processes underpin local community dynamics that form an important component of biodiversity change (e.g., Figure 2.4; Vellend, 2010, 2016).

Abundance-related metrics (composition, total and relative abundance; see box 1) are expected to be most responsive to changes in selection processes acting on communities. For example, under changing environmental conditions, deterministic fitness differences between individuals within a population alter birth and death rates (i.e., demographic effects). This has consequences for population dynamics, and populations within a community increase or decrease in abundance. When species differ in the effect of these selection-based changes, variation in population dynamics between different species within a local community occurs. These population changes manifest themselves as changes in composition and relative abundance.

In contrast to selection processes relating to abundance metrics, changes in species richness and identity are expected to be sensitive to environmental changes that alter movement community processes: The immigration or emigration of individuals (either active or passive – e.g., migration or dispersal) into or out of a local community adds or removes species from a community. Most examples of movement mediated richness change come from colonisations of novel species on islands (i.e., MacArthur & Wilson, 1967), many of which are driven by human actions in recent times (Sax & Gaines, 2008; Vellend *et al.*, 2017). Furthermore, the capacity for species to disperse into communities as they assemble affects climax or equilibrium community richness (Lichter, 2000; Makoto & Wilson, 2016). Batt and colleagues (2017) reported a novel example from marine benthic fish assemblages in which increasing range size of rare and transient species, through movements to new localities, increased the species richness of any given location within a region.

Movement can also cause additional selection processes by creating interactions between arriving species and those present in the local assemblage and therefore drive additional community changes (Gilman *et al.*, 2010; Urban *et al.*, 2012; Alexander *et al.*, 2015; Vellend, 2016). For instance, Alexander and colleagues (2015) found that transplanting competitors into Swiss Alpine plant communities had large effects on the survival, biomass, and flowering probability in species of the local assemblage.

2.5.1 How do community processes respond to specific dimensions of temperature change?

The effects of a change in temperature magnitude (central tendency and variability) on local communities influence the selection process through population birth and death rates, leading to changes in the relative abundance of species found in a community (Figure 2.4). Temperature-related magnitude changes occur through environmental filtering: selection of individuals with higher relative fitness and selection against individuals with low fitness. Changes in temperature magnitude predict biodiversity change, and this, in part, explains why this approach is so commonly adopted. A proximate cause of these community responses is that species often evolve to optimise temperatures frequently experienced, leading to a peak in performance (Angilletta, 2009). In addition, temperature variability can exceed species' limits (e.g., Mckechnie & Wolf 2010; Dowd *et al.* 2015). For example, modeled population trends of water and sea birds across the United Kingdom, based partly on summer and winter temperature extremes, predict 56% of variation in average the population dynamics of birds in this region (Johnston *et al.* 2013).

However, complexities of temperature change in space and time are missed when considering temperature exclusively from this perspective. How the selection and movement of individuals respond to changes in temperature dimensions depends on the spatial and temporal nature of temperature changes (Figures 2.1, 2.3). Considering the dimensionality of temperature leads to different predictions for how biodiversity will change with warming (Ordonez & Williams 2013; Garcia *et al.* 2014, described in Figure 2.4).

2.5.2 Local scale shifts in temporal position and availability

The temporal position and availability dimensions of temperature change affect local community selection processes. Shifts in temporal position (e.g., seasonality and the earlier onset of spring, Figure 2.1) and temporal availability (e.g., duration of temperatures above a physiological threshold, Figure 2.1) drive demographic change (Jones & Wiman 2012; Gaillard *et al.* 2013; Matechou *et al.* 2014; Figure 2.4). For instance, variation in spring timing (temporal position) between years reduced roe deer (*Capreolus capreolus*) population growth rates by limiting successful spring recruitment (Gaillard *et al.*, 2013). In another example, broods in common blue butterfly (*Polyommatus carus*) populations emerged later at higher latitudes, because of differences in the availability of spring and summer temperatures. This change in temporal availability constrained the total broods within the year at northern sites, leading to a smaller overall population size (Matechou *et al.*, 2014).

In ecosystems with seasonal cycles in temperature, a key indirect driver of community change is the mismatch in timing of life history events for species with strong dependencies. This effect is exacerbated if entire groups of species that interact have different capacities to respond to temporal position or, if changes to temporal availability alter how life-history stages transition (i.e., development times). Compelling examples are known of mismatches among resources, consumers, and predators. In a now classic example, Both and colleagues (2009) found that, for passerine birds, climate change led to advances in temporal position of caterpillar prey peak abundance that were unmatched by changes in peak food demand. The predators of these passerine birds did not shift the date of their energy requirements to keep pace with changing prey fledgling availability, and therefore, mismatches occurred at multiple levels across an ecological assemblage (Both *et al.*, 2009). Similar mismatches in key seasonal timings across trophic levels were found with climate change for 726 plant, vertebrate and invertebrate taxa in the United Kingdom (Thackeray *et al.*, 2010). Large-scale compositional changes are expected to occur in communities undergoing mismatches in the timings of species present, because mismatches lead to performance (and abundance) declines of species lacking the resources required within in a specific time window.

2.6 Change in spatial dimensions of temperature change through time

The distance between habitat patches and habitat area are two key components of spatially explicit ecological theories, such as metapopulation patch dynamics (Hanski, 1998) and island biogeography (MacArthur & Wilson, 1967). Parallels can be drawn for spatial temperature dimensions. For example, temperature availability relates to patch or island size, and temperature position relates to interpatch distances or island distance from a mainland. I use analogous ideas to explore the changing position and availability of temperature in generating community dynamics.

2.6.1 Spatial availability

Temperature spatial availability measures the geographic area of temperature (i.e., spatial extent) within species' niche limits (Figure 2.3). The effects of changing temperature spatial availability are dependent on scale. At a local scale, selection processes in communities determine change because temperature availability at a local scale can be viewed as an ecological resource (Magnuson *et al.*, 1979; Roughgarden *et al.*, 1981) for which individuals compete (Melville, 2002). Therefore, individuals' performance and population abundance can be affected by changing geographic area of thermal resources and habitat patches (Matthiopoulos *et al.*, 2015). For example, fragmentation of primary forests leads to patches of matrix that can be many degrees warmer than contiguous forest (Senior *et al.*, 2017), and the size of these warm patches is expected to influence the space use, behavior, and survival of populations of species dependent on forest habitats (Tuff *et al.*, 2016).

At regional to global spatial scales, the available area of thermal niche limits species geographic range sizes and, therefore, a species' global abundance as the two are strongly linked (Borregaard & Rahbek, 2010). Limited availability of areas within the limits of the thermal niche leads to an increased probability of extinctions if populations shrink in geographic area and abundance (Purvis *et al.*, 2000). As such, for a regional community, selection processes are important because the geographic extent of a preferred climate directly constrains species range extents, which deterministically affects species abundances. In the Pleistocene, a period of rapid temperature changes, species' extinctions occurred at higher rates in regions in which climate refugia were not sufficiently large to maintain viable populations (e.g., Hofreiter & Stewart 2009; Nogues-Bravo *et al.* 2010). In this period, species with large body sizes were particularly sensitive to temperature availability change because of low density and large ranges (Lyons *et al.*, 2004; Barnosky, 2008). The polar bear (*Ursus maritimus*) provides a modern analogue of a species with increased risk of population extinctions due to spatial availability of temperature-dependent habitat. For this species, there is a predicted 68% reduction in summer habitat availability by the end of the century (Durner *et al.*, 2009).

The spatial context of changes in temperature availability, rather than aggregated temperature data alone, provides additional insights to community responses to temperature change. As one example, if there is greater geographic area of temperature available, at either local or regional scales, we expect populations in environments of more optimal temperatures to increase in size, potentially increasing the total abundance of a community too (Cline *et al.*, 2013). This prediction requires testing in model systems

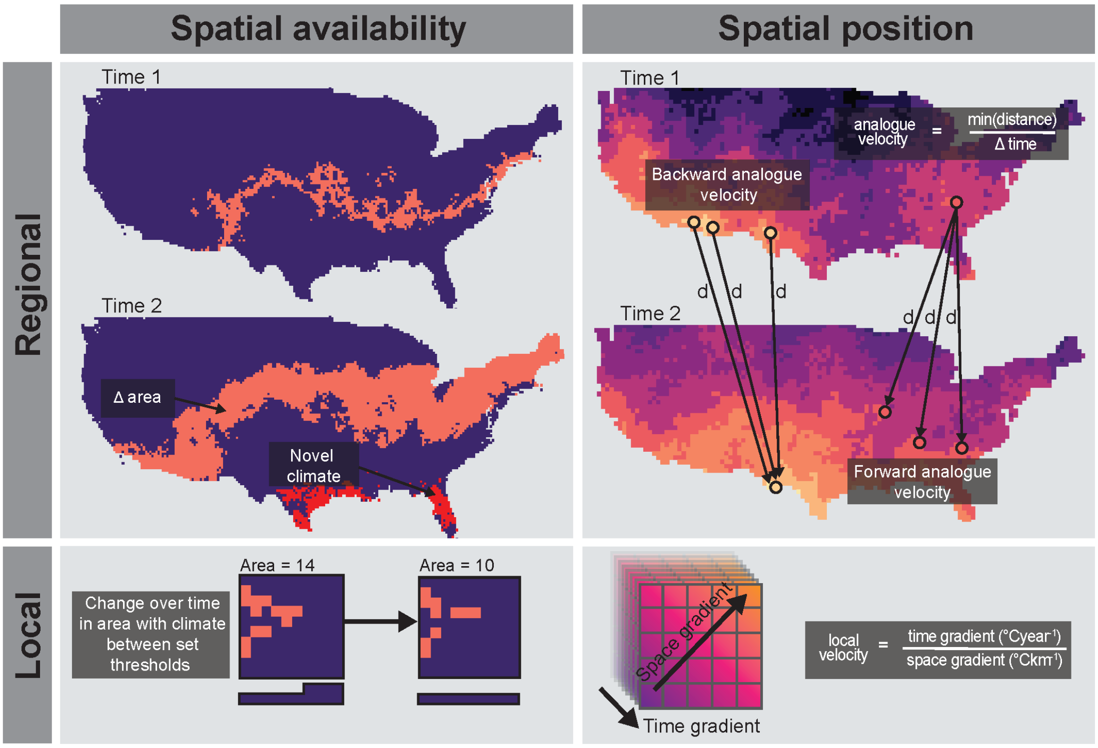

Figure 2.3 Schematic diagram of spatial dimensions of temperature change. Spatial availability is represented in the present chapter as differences in the total geographic area of thermal niche at a regional scale. Novel climates may emerge, representing newly available temperature regimes. Spatial position can be measured as forward or backward temperature velocity, which are proxies for different ecological processes of emigration and immigration respectively (Carroll *et al.* 2015, Hamann *et al.* 2015). Analogue velocity is the minimum distance necessary to travel to maintain constant temperature conditions (Hamann *et al.* 2015). Local climate velocity is the rate of temporal change in temperature over the spatial gradient of temperature (Loarie *et al.*, 2009). Adapted from Garcia *et al.* 2014 and Carroll *et al.* 2015.

that disentangle the area of temperature availability from habitat size more generally. Figure 2.5 provides a visual representation of multiple dimensions of community responses, using species- and rank-abundance distributions and community temperature index. These predictions are in contrast with mean temperature change, which predicts that different species may decrease or increase in abundance depending on which thermal habitats are preferred by individuals, such that total abundance may not increase (locally or regionally; Johnston *et al.* 2013). Sampling more individuals (with increased temperature availability) increases variation of community traits from sampling effects alone (i.e., increase variation in species thermal affinities but no directional shift in community average thermal affinity as would occur with mean warming). Richness will increase if movements into communities are concurrent with greater area of temperature available, through species-area effects (Brose *et al.*, 2004).

A special case of spatial availability change is the emergence of a novel climate (Williams *et al.*, 2007; Ordonez & Williams, 2013). Novel climates can be considered new temperature regimes that were globally unavailable during the evolution of species in the regional fauna, as have occurred frequently throughout Earth’s geological history. Given that the size of available climates is limited by the size of the planet, an area of novel climate space must exclude or replace an area of present-day climate space. Within novel climate space, no-analogue species assemblages are expected to form with corresponding shifts in species composition through time because of interspecific differences in climate tolerances (Williams & Jackson, 2007). The ecological implications of emerging novel climates are extremely difficult to anticipate, and ecological surprises are expected to unfold with new species interacting for the first time (Radeloff *et al.*, 2015).

2.6.2 Spatial position

A change in temperature spatial position measures the geographic distance a specific temperature (thermal isocline) shifts after a climatic change (i.e., spatial distance in kilometers). Temperature velocity, the rate of spatial shift in thermal isoclines (Figure 2.3; measured as the rate per km per decade), is a frequently used metric to measure changes in the spatial position (Loarie *et al.*, 2009; Hamann *et al.*, 2015). Therefore, the movement of individuals is an important mechanism underpinning community responses to this temperature dimension. For example, individual leatherback turtle (*Dermochelys coriacea*) movements tracked 15-degree-Celsius isotherms (McMahon & Hays, 2006), and shifts in species ranges are also well documented and are increasingly predicted to track the position of preferred temperatures with warming (Devictor *et al.*, 2008, 2012;

Burrows *et al.*, 2011; Pinsky *et al.*, 2013; Hiddink *et al.*, 2015; Sunday *et al.*, 2015). Pinsky and colleagues (2013) demonstrated that range centroids have tracked the position of thermal isoclines with climate variability in the last 50 years in 360 marine taxa.

Identifying whether individuals move within or outside of their geographic range is also important when interpreting biodiversity change (Lenoir & Svenning, 2015). Movement outside of a geographic range – that is, colonisation of a new habitat – will result in species richness and species identity change for a receiving community (see the tail of rank-abundance distributions in Figure 2.5g). These initially rare species may become more common over longer temporal scales because of increases in population sizes (in Figure 2.5g, the rare species shift leftward in rank abundance distributions). Conversely, shifts in spatial position can lead to richness declines when extirpations of individuals emigrate from communities, which result in local absences (independent of selection processes altering birth and death rates). The direction of the richness change depends on the relative positioning of species' range edges across the community. Communities receive species that are on a leading range edge but lose species at a contracting range edge. Shifting isotherms may also elicit species relocations within ranges, and therefore, the relative abundances of species is expected to shift to follow these isotherms. This process could act independently of local abundance change driven by a change in temperature magnitude and selection processes (Figure 2.4).

Species traits cause variation in individuals' response to the position dimension of temperature change, implicating the importance of trait-based metrics (e.g., Sunday *et al.* 2015). For example, at the community level the average species' thermal affinity in a community, often summarised as a community temperature index, is expected to be sensitive to the spatial position dimension of temperature change (Figure 2.4). With the establishment of warmer tolerant colonists, the community temperature index is expected to increase and the distribution of species' thermal affinities to become increasingly right skewed (Figure 2.5h; ter Hofstede *et al.* 2010; Bates *et al.* 2014b). This is in contrast to predictions from changes in temperature availability, according to which only increased variation but no mean change in species thermal affinities is expected (Figure 2.5d cf. 2.5h). Furthermore, species with high mobility have better capacity to keep pace with spatial shifts in isotherms (Sunday *et al.*, 2015).

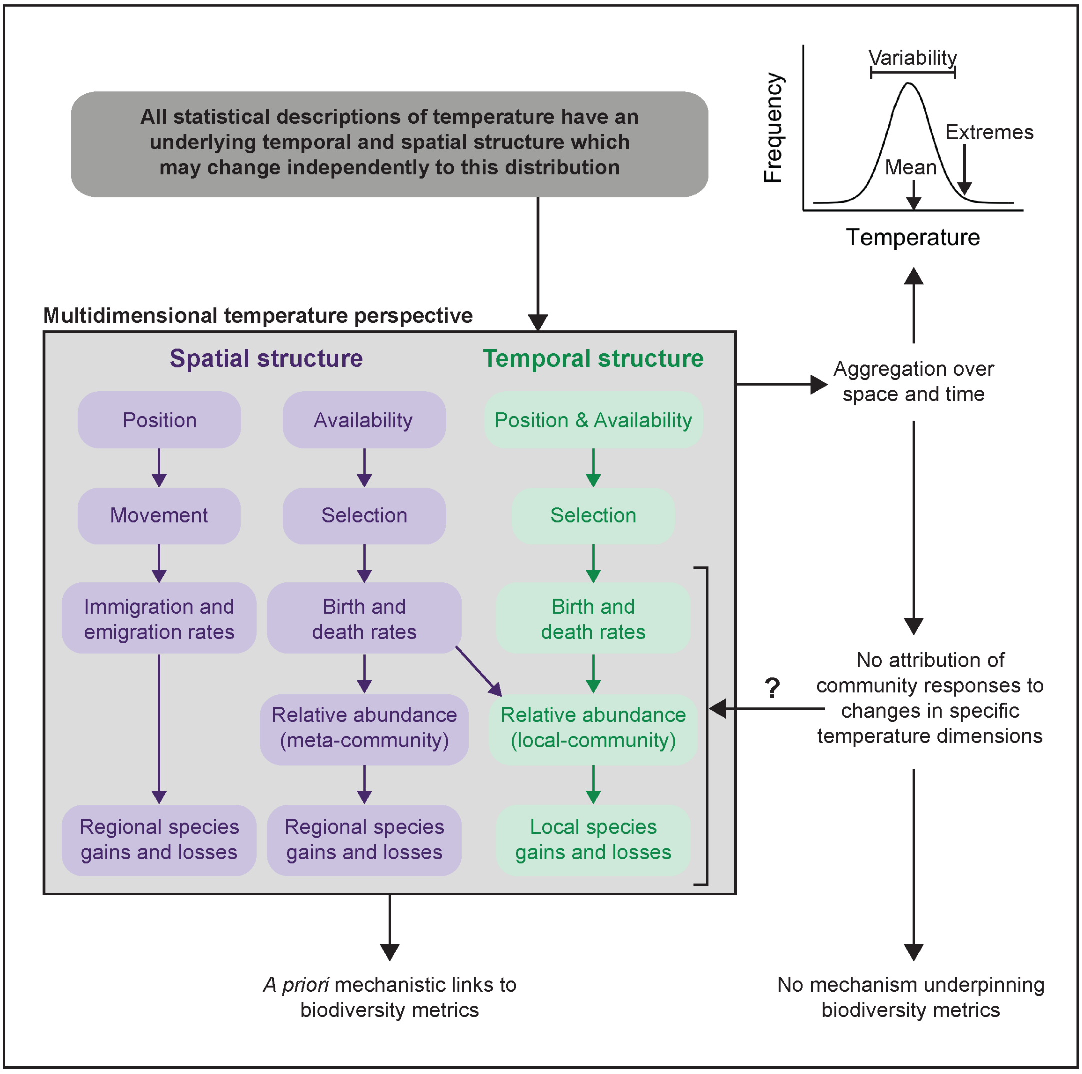

Figure 2.4 Framework linking changing temperature dimensions to processes that drive community level responses. Applying a multidimensional perspective explicitly accounts for temperature changes in space and time that affect biodiversity that occurs through selection and movement pathways. Population level effects arise when selection influences birth and growth rates, and movement influences immigration and emigration rates. Changes in population and demographic rates drive changes in the relative abundances and richness of regional and local communities. If we aggregate temperature over space and time, we miss the opportunity to attribute community responses to changes in specific temperature dimensions. We also lack the resolution to build a priori hypotheses with mechanistic links between changes in the physical environment and individuals' responses.

2.7 Can a multidimensional perspective help disentangle pathways of community change?

Here, I illustrate how two important biodiversity responses to environmental change – community homogenisation and local richness change (Dornelas *et al.*, 2014; McGill *et al.*, 2015) – are driven by fundamentally different pathways, rarely disentangled in the literature. I further discuss the potential for disaggregation of communities through time – a community response to climate change that can only detected by studying the effects of temporal rather than spatial dimensions of temperature change.

2.7.1 Disentangling community homogenisation

Communities are generally becoming more similar in composition in time or space – a process called homogenisation – often quantified as reduced beta diversity (Jurasinski & Kreyling, 2007; Baiser *et al.*, 2012; Davey *et al.*, 2012; Avolio *et al.*, 2015; Magurran *et al.*, 2015; Savage & Vellend, 2015). Identifying the specific dimension of temperature change leading to community homogenisation has potential to help estimate the distinct effects of community abundance shifts (selection processes) versus species range shifts or expansions (movement processes, Figure 2.4).

Selection processes cause community homogenisation through time when a subset of species in a local assemblage systematically increase or decrease in abundance. For example, across many local stream-fish assemblages in France, temporal changes in community composition were related to losses of individuals – and, therefore, population declines and relative abundance changes – which has favoured an increasingly similar set of species since the 1980s (Kuczynski *et al.*, 2017). In this case, community homogenisation was linked to selection processes and the timing dimension of temperature change emerged as an important predictor.

Through space, homogenisation will occur when the same subset of species increasingly occupy many local communities across a region. For this to occur, species distributions must expand or contract by movement within a region. If range-shifting species display coordinated expansions or contractions across communities then spatial homogenisation is expected. This form of homogenisation is often driven by movement of generalist species undergoing a range expansion (Davey *et al.*, 2012). In cases in which movement processes drive homogenisation, species richness will also increase (La Sorte, 2006; Davey *et al.*, 2012; Batt *et al.*, 2017). However, the role of temperature position driving homogenisation and richness is often unexplored (Davey *et al.*, 2012; Savage & Vellend, 2015). A pressing debate is the simultaneous stability of richness with ongoing biotic homogenisation of communities (i.e., Magurran *et al.* 2015 cf. Savage & Vellend, 2014) and reordering of communities (e.g., Jones *et al.* 2017). This debate will benefit if the multiple dimensions of temperature change are identified in studies testing theory.

2.7.2 Drivers of local richness change

Local species richness change is commonly attributed to the magnitude dimension of temperature change (Menéndez *et al.*, 2006; Britton *et al.*, 2009; Davey *et al.*, 2012; Tayleur *et al.*, 2016). However, increases in richness must occur because of species movements (i.e., local colonisations), whereas decreases can be due to selection (i.e., decline in situ) or movement (i.e., movement away from site). The rate that species move into a warmer (increased temperature magnitude) environment is determined in part by the position dimension of temperature change, but this could trade-off with greater species losses as warmer temperatures exceed species tolerance limits. Few studies, if any, have acknowledged the interaction between these two processes in driving species richness change.

2.7.3 Community temporal disaggregation from changes in temporal position and availability of temperature

Assessing community level responses to changes in timing dimension of temperature has revealed a distinct fingerprint on community composition, independent of changes in mean temperature. Specifically, Thomsen and colleagues (2015) found that with changing temporal position and availability of temperature, growing seasons are longer causing earlier springs and longer summer periods (these two dimensions were correlated in this study). These temperature changes affect the seasonal timing of peak abundances in the warm and cool affinity species differently. Warm species had later peak abundances, whereas cool species had earlier peak abundances (Figure 2.6a). If communities have varying degrees of thermal niche complementarity – that is, high variation in thermal performance optima (Figure 2.6b) – the temporal synchrony of species may breakdown. The extent of asynchrony will depend on species thermal trait distributions across the community (Figure 2.6c). Long-term and high resolution community time series are necessary to estimate the effects of temporal dimensions of temperature change, which may explain our gaps in understanding of community responses to this temperature dimension (Magurran & Henderson, 2010; Thomsen *et al.*, 2015).

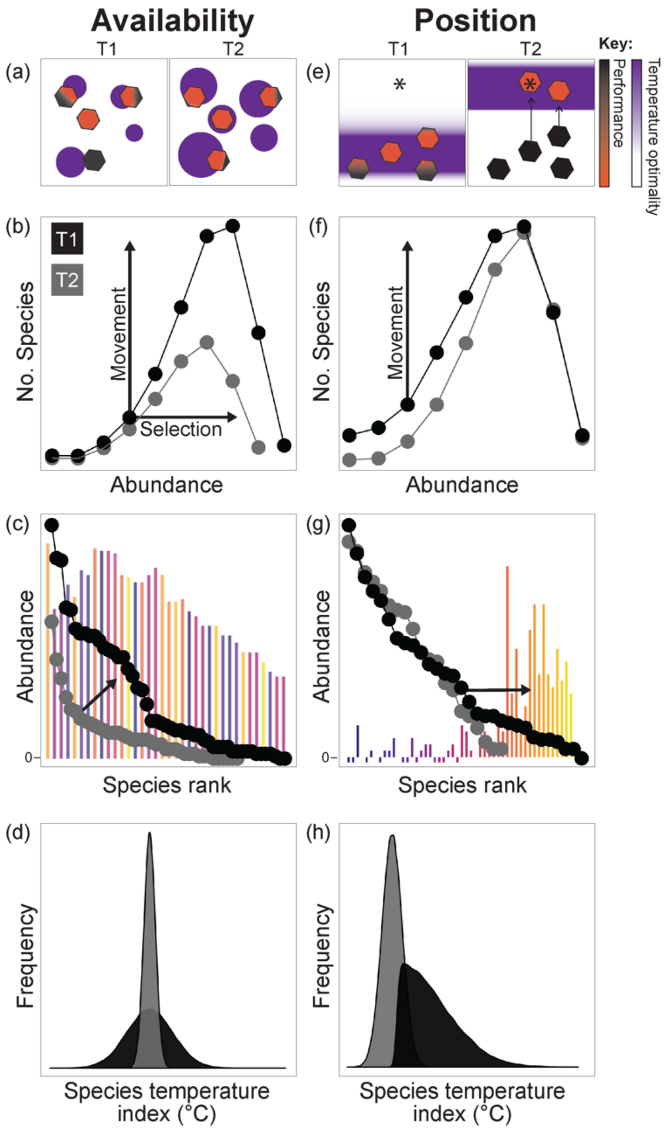

Figure 2.5 Schematic diagram linking changes in spatial availability and position of temperature with community responses using different biodiversity metrics. In panels (a) and (e), the polygons represent individuals, and the purple (dark) regions represent areas of temperature optimality. In panels (b) and (f), species abundance distributions show a right shift in central tendency with increased abundance, an increase in height with increasing richness. In panels (c) and (g), rank abundance distributions show an increasing tail with higher richness and a shift right with increasing total abundance. Note the long tail for temperature position change. The underlying bars represent species abundance change between time points but maintained at the rank on the x-axis in time point 1. The colours refer to thermal traits (purple (dark) is cool affinity; yellow (light) is warm affinity). In panels (d) and (h), changes in the distribution of species' thermal affinities between time points is the mean of this distribution. Note the same mean for changes in spatial availability and the long tail and changing mean for spatial position.

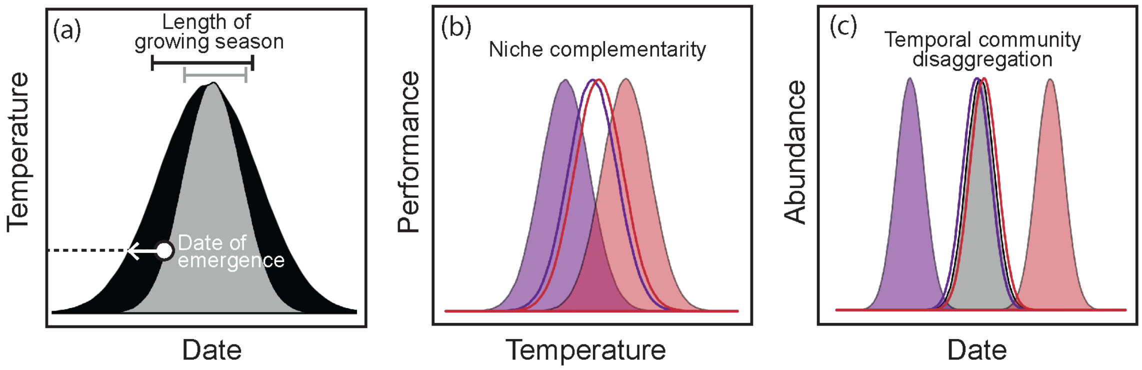

Figure 2.6 This schematic suggests how a community's response to temperature timing depends on the extent of overlap between thermal niches. (a) Temperature thresholds (the dashed line) for key demographic and physiological processes result in defined dates of first emergence and lengths of growing season, from time 1 (grey) to time 2 (black); changing the timing of temperature dimensions causes earlier emergence dates and an increased length of growing season. (b) Species niches in a community overlap to different extents; for example, niche complementarity is low in filled species thermal performance curves or niche complementarity is high in unfilled species thermal performance curves. (c) These differences result in community disaggregation between the timing of peak abundance for warm and cool species, as a result of the timing changes shown in panel (a).

2.8 Conclusions

Similar ecological patterns can arise from different combinations of processes (Lawton, 1999). I suggest this is also true when measuring community responses to environmental change. To understand biodiversity change on a warming Earth, we must link spatial and temporal structure of temperature and community change – short of this, misattribution of the climatic processes responsible for biodiversity change may occur. Similar community changes can occur through both selection and movement pathways; biodiversity forecasts and management decisions may depend on the relative importance of each. Characterising the dimensionality of how temperature is changing at scales relevant for biodiversity processes will require closer collaboration between physical scientists and ecologists. This will hopefully lead to an attribution of temperature's effects beyond average temperature change. This chapter demonstrates a need to build these mechanistic connections into how physical regimes affect biodiversity change, being explicit in space and time.

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Chapter 3 The shape of abundance distributions across temperature gradients in reef fishes

This chapter formed the basis of the publication:

Waldock, C., Stuart-Smith, R.D., Edgar, G.J., Bird, T.J. & Bates, A.E. (2019). The shape of abundance distributions across temperature gradients in reef fishes. Ecol. Lett., 22, 685–696. DOI: 10.1111/ele.13222

3.1 Abstract

Improving predictions of ecological responses to climate change requires understanding how local abundance relates to temperature gradients, yet many factors influence local abundance in wild populations. I evaluated the shape of thermal-abundance distributions using 98 422 abundance estimates of 702 reef fish species worldwide. I found that curved ceilings in local abundance related to sea temperatures for most species, where local abundance declined from realised thermal ‘optima’ towards warmer and cooler environments. Although generally supporting the abundant-centre hypothesis, many species also displayed asymmetrical thermal-abundance distributions. For many tropical species, abundances did not decline at warm distribution edges due to an unavailability of warmer environments at the equator. Habitat transitions from coral to macroalgal dominance in subtropical zones also influenced abundance distribution shapes. By quantifying the factors constraining species’ abundance, I provide an important empirical basis for improving predictions of community re-structuring in a warmer world.

3.2 Introduction

Amongst the most fundamental questions in ecology is how an organism’s performance is affected by gradients in environmental conditions. Ecological performance (e.g. fitness, demographic rates, abundance, occupancy) in geographic space is often difficult to attribute to environmental variation because many entangled processes act at once (Gaston, 2009; Pironon *et al.*, 2016). Given the importance of temperature in structuring life across biological scales, from biochemical reactions to organism behaviour and species’ interactions (Dell *et al.*, 2011), characterising the role of temperature in driving realised ecological performance is essential for predicting species’ responses to warming and environmental variability (Deutsch *et al.*, 2008).

Species' abundance is expected to be greatest at the centre of their environmental niche if performance declines outside of particular 'optimal' environmental conditions (Brown *et al.*, 1995; Pironon *et al.*, 2016). Many explanations exist for this 'abundant-centre' effect, with mechanisms operating from small to large scales (e.g. physiology, environmental auto-correlation, Brown, 1984; Pironon *et al.* 2016). However, assumptions underlying abundant-centre effects have been questioned for decades, and can be violated due to various ecological and evolutionary factors including: (1) fine-scale environmental heterogeneity, (2) local adaptation, (3) physical barriers to dispersal truncating geographic ranges, (4) geographic availability of niche space, (5) habitat gradients and (6) species' interactions (Sagarin *et al.*, 2006). Therefore, the distribution of abundance across environmental gradients is often complex, and abundance patterns have frequently been inconsistent with the abundant-centre hypothesis (Sagarin & Gaines, 2002; Pironon *et al.*, 2016; Dallas *et al.*, 2017; Santini *et al.*, 2019).

Moreover, it may be unrealistic to assume that species from tropical and temperate systems – which experience markedly different temperature regimes – will display similar abundance structure across thermal gradients. For example, abundance may peak closer to warm thermal distribution edges when temperature variation is low, such as the tropics. Tropical species investigated generally have narrow thermal safety margins – they live nearer their thermal upper limits for physiological and demographic rates (Angilletta *et al.*, 2010; Morley *et al.*, 2012). In contrast, temperate species experience higher seasonal and short-term temperature variation and may have optimal temperatures below upper limits.

Compelling ecological and physiological hypotheses predict the shape of abundance across thermal distributions, but defining the peaks and edges of thermal distributions presents practical challenges. Both require high-resolution survey data across large spatial scales (Bates *et al.*, 2015a; Knouft, 2018). Abundance data are highly variable and strongly affected by sampling errors and biases. Sites of similar temperatures frequently differ in many other factors affecting local abundance. Thus, the influence of temperature may not be obvious when examining mean local abundance. Instead, a signal may be more easily detected from upper abundance limits, given enough data (Cade & Noon, 2003; Vanderwal *et al.*, 2009), and more compelling tests of abundant-centre effects have been described by modelling maximum abundance (Langlois *et al.*, 2012; Knouft & Anthony, 2016; Martinez-Gutierrez *et al.*, 2018).

Here, I use the Reef Life Survey (RLS) data – a standardised, well replicated and globally distributed species-level census of whole shallow reef fish communities – to overcome data consistency and sample size issues which have been prohibitive in previous analyses. First, I empirically quantify the variation in abundance across 702 species' thermal distribution using multiple approaches – I call this the 'thermal-abundance distribution'. Second, I test for systematic differences in the shape of thermal-abundance distributions in fishes from tropical vs. temperate guilds, accounting for limitations due to habitat availability. Overall, I find abundance is consistently related to temperature, with peaks in performance indicating existence of 'thermal optima' for ecological performance. The position of species' peaks along temperature gradients varies, however, resulting in skewed thermal-abundance distributions, with a majority of species that are most successful between the centre to warm-range edges.

3.3 Materials and methods

I evaluated the thermal-abundance distribution for individual reef fish species and quantified how many species showed abundant-centre patterns vs. asymmetrical or 'no-trend' shapes (3*.3.2 Categorical assessment of thermal-abundance distribution shape*). I then standardised abundance and temperature across all species' geographic ranges and analysed the mean shape of thermal-abundance distributions (*3.3.3 Quantifying the average shape of thermal-abundance distributions*). Finally, I modelled variation between tropical and temperate guilds in the shape of species-specific thermal-abundance distributions (*3.3.4 Quantifying structure in the thermal-abundance distribution shape*). See Figure 3.1 for a schematic of all analyses.

3.3.1 Data sources

The abundances of all fishes present along transects were counted by trained RLS participants between 2007 and 2016 (Figure 3.2) following strict data quality controls (Edgar and Stuart-Smith 2014, http://www.reeflifesurvey.com). For each species, the abundance for non-cryptic/adults individuals (>40% maximum body length, Froese and Pauly 2000) was summed within individual transects, and then averaged among transects at each RLS 'site' (minimum 200 m apart) providing site-level mean densities per 500 m^2. Species with <30 abundance records or an observed thermal range of <3°C (mean sea surface temperature; see below) were deemed to have inadequate data for the modelling approaches used here. This gave us 98,422 abundance estimates for 702 fish species at 3,120 sites. I defined species' absences from a circular buffer with a radius

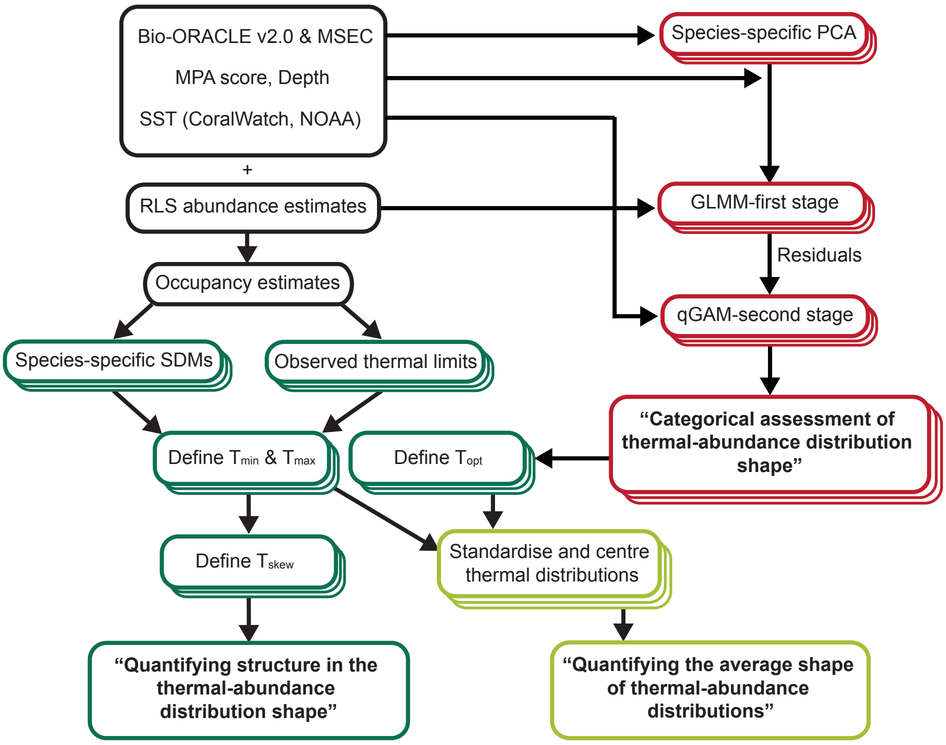

Figure 3.1 Schematic diagram outlining data and analyses used in the manuscript.

Stacked nodes indicate each species is treated independently.

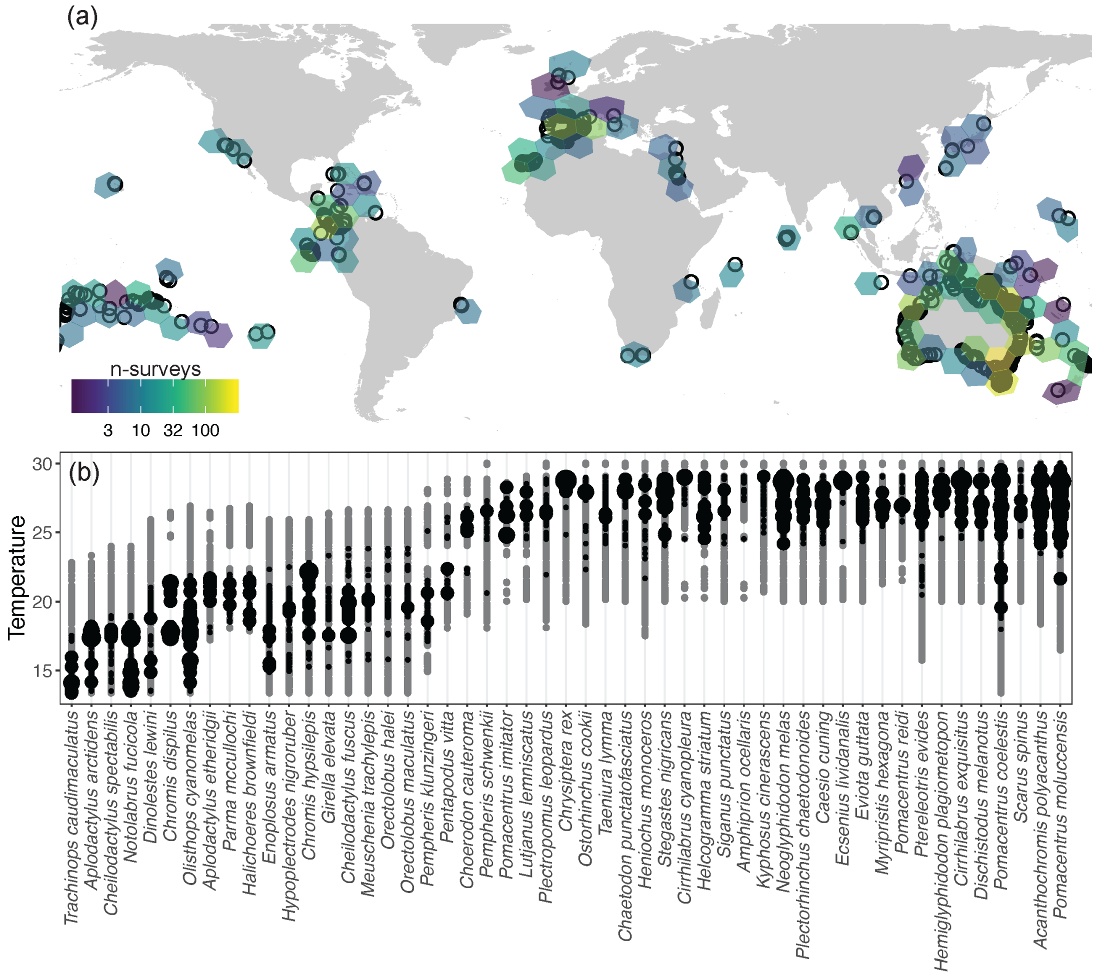

Figure 3.2 Distribution of Reef Life Survey (RLS) sites across geographic and thermal gradients. (a) Geographic distribution and intensity of RLS sampling used in these analyses; sites across the globe are aggregated to equal area hexagons (n = 3132 sites). Points show distribution of RLS sites. (b) Sampled thermal distributions (grey points) relative to occurrences (black points) for 50 example species, sampling often extends beyond range edges.

of 10° latitude/longitude around each RLS site, recording zero abundance at sites surveyed at which (1) the species was not observed, but (2) was observed elsewhere within this buffer (Bivand & Rundel, 2018). While lack of observed presence may not be a 'true absence', they represent locations at which a given species was in insufficient local abundance to have been detected in the standardised surveys. This resulted in a total of 781,983 observations for analysis.

I matched the location of each site with sea surface temperature (SST) values at a ~5 km^2 scale (NOAA Coral Reef Watch, 2018, see Appendix 3: Figure S2 and S3 for comparison to additional SST resources and metrics). I calculated 2-year mean annual-site temperature from daily SST records. This period covered the influence of temperature on individual survival and recruitment processes over multiple generations, which in turn influences population size. Covariate data were obtained from the Marine Socio-Ecological Covariate dataset (Yeager *et al.*, 2017) and Bio-ORACLE v2.0 *(*Assis *et al.* 2018, see Appendix 2: Table S1). In addition, I estimated species-specific habitat associations using the total % cover of macroalgae or live coral from 20 photo quadrats from the same transects surveyed for fishes. I estimated mean transect depth from multiple surveys to obtain a site average depth. Finally, thermal guilds were defined from the peak of modelled maximum abundance (T_{opt}, see *3.3.2*). Species were considered 'temperate' when T_{opt} <23°C and 'tropical' when T_{opt} >23°C based on the naturally occurring thermal guild separation previously observed by Stuart-Smith *et al.,* (2015, 2017).

For all species, I estimated semi-quantitative scores for confidence in values of T_{opt}, and the minimum and maximum temperatures at range limits (T_{min} and T_{max}). Methods for confidence scores are provided in online supporting materials (Appendix 2) and the derivation of T_{opt}, T_{min} and T_{max} are described in sections *3.3.2* and *3.3.4*. Sensitivity analyses with only 'high-confidence' species (*n*=181 species) supported the main results.

3.3.2 Categorical assessment of thermal-abundance distribution shape

I used a two-stage residual analysis to model abundance variation across each species range to handle the effects of multiple covariates on abundance without risk of model overfitting - thereby also retaining a focus on the effects of temperature. I first accounted for the influence of covariates, other than temperature, using generalised linear models fitted with a zero inflated-Poisson (ZIP) error structure. For each species independently, I ran species-level principal component analyses (PCA) including factors related to water chemistry (e.g., O_2, phosphate, nitrate), oceanography and bathymetry (e.g., current velocity), ecology (e.g., productivity, reef area) and human pressures (e.g., human population density) amongst others (see Appendix 2: Table S1). I used PCA because the goal of the first-stage analysis was to account for as many of the factors as possible that potentially affected each species' local abundance before I tested the effect of temperature – I did not test for the specific effect of each covariate. PC1 were related to site temperature, and therefore it is important to first account for these sources of covariation to identify the independent influence of temperature on abundance. To avoid model overfitting, for each species I only included PCA axes explaining >10% environmental variation experienced by species across their range. In addition to these PCA axes derived independently for each species, I also included several other covariates in the first stage models: site depth, protection status scores (Edgar *et al.* 2014) and sampling intensity (calculated as the number of survey sites sampled per degree temperature across a species' geographic range). Across all RLS sites, the most important sources of environmental variation were human population density, reef area, dissolved-O_2 and productivity (see Appendix 3: Figure S4).

For each species I extracted the residuals from the first-stage models, and then modelled the relationship between temperature and residual-abundance using quantile generalised additive models in the R package 'qgam' (Fasiolo *et al.*, 2017). The use of generalised additive models rather than linear models allowed a flexible fit to highly variable abundance data. I fitted temperature as a smooth term at the 80th quantile of residual-abundance, thus I modelled maximum residual-abundance without needing to estimate maximum abundance within a temperature 'bin'. I used k=4 degrees of freedom in the regression splines so that models were robust to outliers and fitted curves were constrained, to some extent, in non-linearity. I also limited the number of absences in each species to equal the number of abundance records. Absences are far more frequent and could overwhelm the shape of abundance distributions, the number of absences also varied by orders of magnitude between species so this approach balanced the number of presences vs. absences for each species. When absences were constrained, I bootstrapped predictions by re-running models to random absence subsets 25 times to avoid spurious estimates of T_{opt} that depended on which absences were excluded. I defined the T_{opt} of each species as the temperature of peak abundance (Figure 3.3). In a test of robustness, T_{opt} values derived from models including and excluding covariates (i.e., a one-stage analysis) were highly correlated with a slope of 1.03 ± 0.01 (r^2=0.90, Appendix 3: Figure S5). For each species, I tested for the presence of spatial autocorrelation in model residuals by comparing correlations between site pairwise distances and residual Euclidean distances using Mantel tests with 999 permutations. Correlations between these two distance matrices were, on average, very weak (0.08±0.08). Thus, type-1 errors are unlikely to be inflated due to underestimated number of degrees of freedom. Including a spatial auto-correlation term when covariates are highly auto-correlated can lead to a focus on local factors driving abundance, here I retain a focus on large scale covariates (i.e., temperature) by not including a spatial auto-correlation term in the final models (Diniz-Filho *et al.*, 2003).

From these models I defined four thermal-abundance distribution shapes, measured by the drop of abundance at the edges of thermal distributions (Sagarin & Gaines, 2002):

i) *No-trend*: neither thermal distribution edge falls to less than 75% of maximum modelled abundance,

ii) *Abundant-centre*: both thermal distribution edges fall to less than 75% of maximum modelled abundance,

iii) *Warm-skewed*: only warm thermal distribution edge does not fall to less than 75% of maximum modelled abundance,

iv) *Cool-skewed*: only cool thermal distribution edge does not fall to less than 75% of maximum modelled abundance,

I assessed differences in the proportion of species in each group using a chi-squared goodness-of-fit test, and tested whether a threshold of 50% maximum abundance influenced my results.

3.3.3 Quantifying the average shape of thermal-abundance distributions

To quantify the overall shape of thermal-abundance distributions in tropical and temperate guilds I aggregated all species into a single thermal-abundance distribution model. Specifically, this analysis tested whether the decline above and below T_{opt} occurred at comparable rates, even if species thermal distributions were truncated by biogeographic factors. I standardised both x- and y-axes (temperature and abundance respectively) in order to allow comparison of curve shape among species with different absolute values of abundance and different thermal distribution widths. I standardised the width of the thermal distributions among species by scaling temperatures to the mean of $\sigma_{T_{min}}$ and $\sigma_{T_{max}}$ (defined in *3.3.4*). I then centred this distribution by T_{opt} to produce a distribution of temperatures centred on 0 ($T_{opt} = 0$). I standardised the range of local abundances by the maximum abundance across a species geographic range to constrain the absolute height of the T_{opt} peak between 0 and 1. I only used abundance

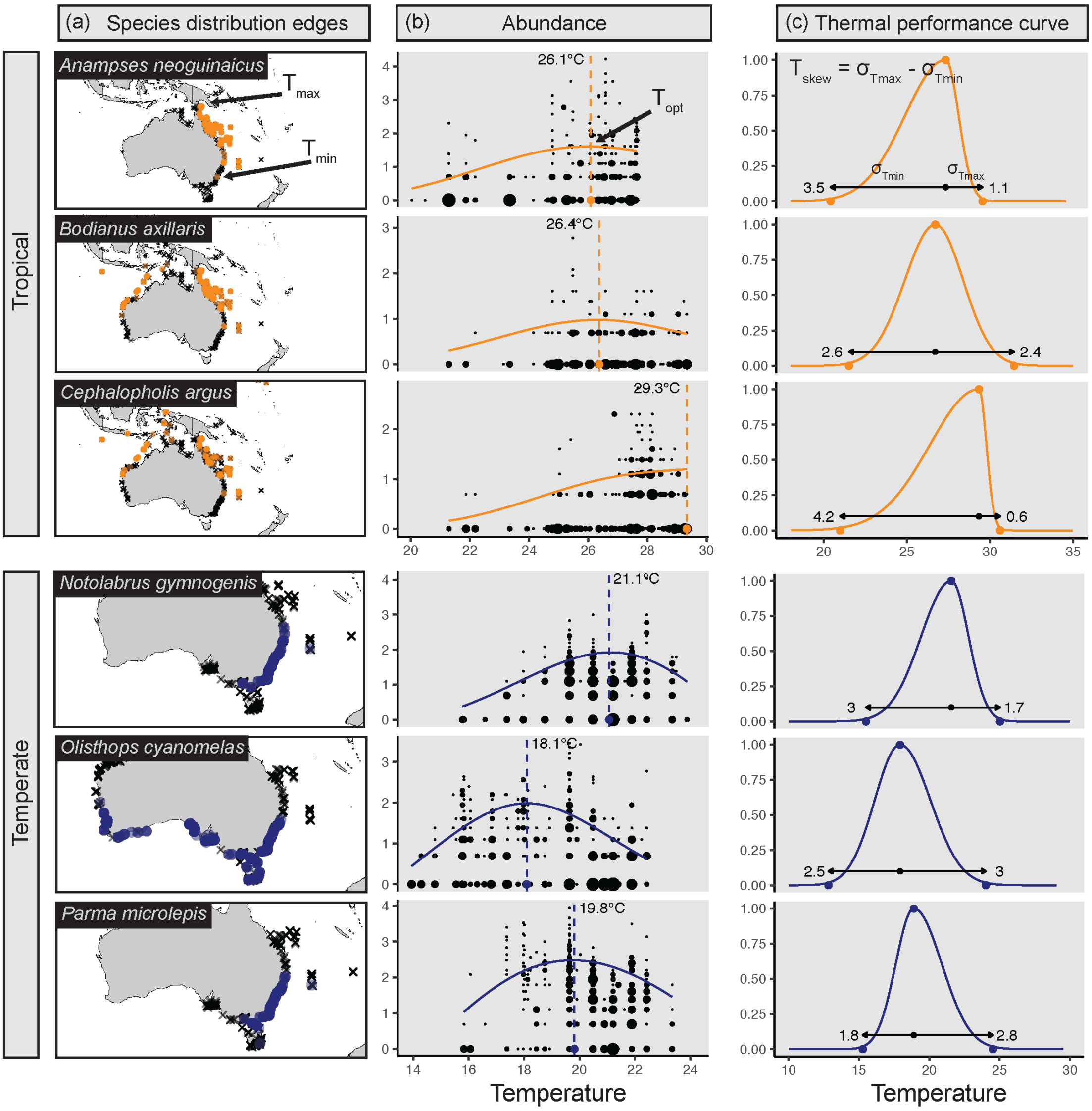

Figure 3.3 Overview of modelling tools and parameters used to characterise the shape of species' temperature-abundance distribution, including example models from the species-specific analysis in tropical (orange) and temperate (blue) guilds. (a) T_{min} and T_{max}, that is, species distribution edges, were derived from species' geographic distributions. (b) Illustrative models conceptualising estimation of T_{opt} which was derived from quantile generalised additive models (qgam) fit to log10 species abundance (note that in main analysis qgam is performed on species' residual-abundance in a 2-stage analysis). Point sizes equate to the number of overlapping points. (c) I use these parameters to define a T_{skew} for 702 species represented by a split-Gaussian function here (see methods and eqn. 1 for full details).

records (i.e. excluded absences). Within each 0.1 temperature bin I estimated, for each species, the 99th percentile of standardised abundance and fitted my model to these maximum abundance values.

Next, I modelled temperature-related ecological performance, Performance(T), directly from the relationship between abundance and temperature (transformed as described above) across all species, using the following split-Gaussian function:

$$\text{Performance}(\text{T}) = \begin{cases} c \times e^{-(\frac{\text{T}-T_{opt}}{\sigma_{T_{min}}})^2} & \text{T} < T_{opt,} \\ c \times e^{-(\frac{\text{T}-T_{opt}}{\sigma_{T_{max}}})^2} & \text{T} > T_{opt} \end{cases} \qquad \text{equation 1}$$

Where T is temperature and *c* is a scaling parameter which defines the height of abundance peak at T_{opt}. This split-Gaussian function modelled abundance as a function of temperature using separate Gaussian functions above and below T_{opt}, the temperature of peak abundance. The rate of change in abundance across thermal distributions is described by separate standard deviations above ($\sigma_{T_{max}}$) and below ($\sigma_{T_{min}}$) T_{opt}. The thermal-abundance distribution shape parameter T_{skew} was estimated as $\sigma_{Tmax} - \sigma_{Tmin}$ from the above equation.

I estimated *c*, T_{opt}, $\sigma_{T_{min}}$, $\sigma_{T_{max}}$ and T_{skew} using MCMC sampling (prior values are provided in Appendix 3: Table S2), and fitted models using JAGS (to provide a flexible framework to define this split-Gaussian functional form) with the package ‘r2jags’ (Su & Yajima, 2012). I fitted models with 4 chains of 10,000 iterations each, a burn-in of 2,500 iterations and a thinning of 5. I visually assessed mixing and stability of MCMC chains for all parameters, as well as confirming that the Gelman-Rubin convergence diagnostic statistic was <1.01 to indicate that models were fully converged. Statistical significance was inferred from assessing the 95% credible interval of parameter posterior distributions. I fitted this model separately to temperate and tropical guilds to obtain simple approximations of thermal-abundance distribution shapes.

3.3.4 Quantifying structure in the thermal-abundance distribution shape

In addition to the qualitative assessment of thermal-abundance distribution shape (i.e., *3.3.2*) and an average thermal-abundance distribution shape for each thermal guild (i.e., *3.3.3*), for each species I estimated a quantitative continuous parameter of thermal-abundance distribution shape (T_{skew}). This was based on the distance of thermal optima (T_{opt} defined in *3.3.2*) to thermal distribution edges (T_{min} and T_{max} – defined below). Note, this approach assumed species thermal performance followed the shape presented in eqn. 1, an assumption generally well supported in this data (see Results), as well as physiological (Angilletta, 2009; Dell *et al.*, 2011) and ecological (Boucher-Lalonde *et al.*, 2014) models. Here, I assumed the parameters of eqn. 1 can be derived from abundance (T_{opt} in *3.3.2*) and thermal range edges ($\sigma_{T_{min}}$ and $\sigma_{T_{max}}$defined in *3.3.3*) that describe the shape of species' thermal-abundance distributions. The parameters $\sigma_{T_{min}}$ and $\sigma_{T_{max}}$ were derived from T_{min} and T_{max}, i.e., the thermal distribution edges defined from species' distributions as described below. I set the scaling parameter *c* to 1.

3.3.4.1 Deriving T_{min} and T_{max}

T_{min} and T_{max} were estimated from the observed 2.5th and 97.5th quantiles of species thermal distributions for each species (as in Stuart-Smith *et al.* 2017). I also accounted for the influence of seasonality by defining T_{min} and T_{max} as the 2.5th and 97.5th quantiles of minimum and maximum temperatures across species distributions during a 2-year period. Furthermore, I accounted for the influence of additional covariates on T_{min} and T_{max} (and extended species' geographic distributions beyond sampled sites) by fitting an ensemble of species' distribution models (SDMs) for each species (details in Appendix 2). I estimated the 95th quantiles of species' predicted thermal distributions from these models – however, my choice of methods to derive T_{min} and T_{max} had no qualitative influence on the results (results in Appendix 3). Here, I presented results for T_{min} and T_{max} derived from sampling limits only, excluding the influence of seasonality (Stuart-Smith *et al.*, 2017). I assumed T_{min} and T_{max} are the 2.5th and 97.5th quantiles of a normal distribution with a mean of T_{opt}, and that the z-score of this distribution was 1.96. I then defined the thermal distribution parameters $\sigma_{T_{min}}$ and $\sigma_{T_{max}}$, introduced in eqn. 1, as: $\sigma_{T_{min}} = (T_{min} - T_{opt})/1.96$ and similarly for $\sigma_{T_{max}}$.

3.3.4.2 Modelling thermal-abundance distribution skew

T_{skew} ($\sigma_{Tmax} - \sigma_{Tmin}$) was quantified as the imbalance of cool and warm thermal distributions edges from T_{opt}, giving a quantitative estimate of thermal-abundance distribution shape I could model. I follow the terminology of section 3.3.2. That is, where species had T_{opt} closer to warm thermal-distribution edges (T_{max}) I called this 'warm-skewed' and T_{skew} was negative. Where species had T_{opt} closer to cool thermal-distribution edges (T_{min}) I called this 'cool-skewed' and T_{skew} was positive. Where species had T_{opt} in the exact centre between T_{min} and T_{max} the skew value was 0.

I estimated the slope of T_{skew} vs. T_{opt} within guilds, using linear mixed-effects models fitted in R using 'lme4' (Bates *et al.,* 2015, version 1.1-17). I fitted separate models for temperate and tropical guilds. I included T_{opt} as a linear independent variable. Species' coral and algal associations were also modelled as independent variables to account for influences of habitat preferences and the geographic patterns in habitat availability on T_{skew} (Appendix 3: Figure S8, S10). I fitted these covariates as simple additive effects with no interactions. I included taxonomic structure as a nested random intercept of Order, Family and Genus in all models to help account for similarities in traits due to shared evolutionary histories within taxonomic groups. I tested for the influence of these terms by comparing AICc values between models. I also used backwards-stepwise model selection, comparing between model fits using likelihood-ratio tests. In addition to the above models, across all species I tested for the potential of non-linear interactive effect of T_{opt} with habitat association on T_{skew} using generalised additive models, fitting this term using tensor product smooths with the R package 'mgcv' (Wood, 2011) and comparing model fits using AICc values. This modelling approach allowed T_{skew} to be modelled with a non-linear interaction between simultaneous gradients in T_{opt} and species' habitat associations.

Code and data for all analyses are available online (code available at https://github.com/cwaldock1/RLS-ThermalNiche, data available at doi:10.6084/m9.figshare.7218104), all analyses were run using the statistical software 'R' version 3.4.0 (R Core Team, 2017).

3.4 Results

3.4.1 Categorical assessment of thermal-abundance distribution shape

Temperature and maximum abundance were significantly related for 75% of the 702 species included in this analysis. The deviance in maximum abundance explained by temperature ranged between 14% and 63%. Thermal-abundance distributions showed abundant-centre patterns for 25% of species (Figure 3.4), and on average, abundance declined by two-thirds of maximum abundance at these species' thermal range edges. Of the remaining species not fitting my 'abundant-centre' criteria, warm-skewed shapes were common (49%), with fewer cool-skewed (14%) and no-trend (13%) relationships (Figure 3.4; X^2=237, df=3, p <0.001).

Abundant-centre trends were more apparent in widespread species with richest data. Among the 'high-confidence' set of species, there was a more even balance of species having warm-skewed (48%) and abundant-centre (38%) thermal-abundance distribution shapes, with the remaining species displaying cool-skewed (10%) or no-trend (3%) shapes (X^2=100, df=3, p<0.001). Where species are not limited by geographic boundaries at cool range limits (i.e., continental margins for southern hemisphere temperate zones) or 'niche availability' limits at warm range edges (i.e., warmest temperatures in oceans), 97% of species display peak maximum abundances away from the edges of species' thermal distributions (i.e., T_{opt} does not = T_{min} or T_{max}).

I also detected a difference between thermal-abundance distribution shapes in tropical versus temperate guilds. The thermal distributions of tropical species were mostly warm-skewed, whereas temperate species were mostly cool-skewed or abundant-centre (Figure 3.4). At cool-range edges, tropical species generally had lower relative abundance than temperate species, but at warm-range edges temperate species had lower relative abundances than tropical species (Figure 3.4b).

3.4.2 Quantifying the average shape of thermal-abundance distributions

Ecological performance displayed a peak at species' T_{opt} in both tropical and temperate thermal guilds (Figure 3.5). However, ecological performance varied among species within a given temperature bin, and a low proportion of variation was explained by a simple split-Gaussian model with temperature as a single covariate (R^2=0.07-0.09). When modelled as a species aggregated mean ecological performance within temperature bins, a much higher proportion of variation in ecological performance across species was explained by this very simple model (R^2=0.73-0.75). The shape of this relationship was modelled with high confidence as indicated from narrow credible intervals for parameter estimates (Figure 3.5). The overall abundant-centre pattern across all species is underpinned by those species' which display an abundant-centre pattern, combined with species that have warm- and cool-skewed distributions that decline at both distribution edges (but at a similar rate, on average, to the decline of both range edges in abundant-centre species, see inset in Figure 3.5).

The skew in ecological performance was significantly different between guilds. Species in the tropical guild were significantly negatively skewed (T_{skew}=-0.65±0.49), such that T_{opt} is closer to warm thermal distribution edges. The opposite is true for species in the temperate guild (T_{skew}=0.88±0.54).

Species are infrequently observed near their maximum observed abundance, even at 'optimal' temperatures, as shown by the restricted height of the thermal performance

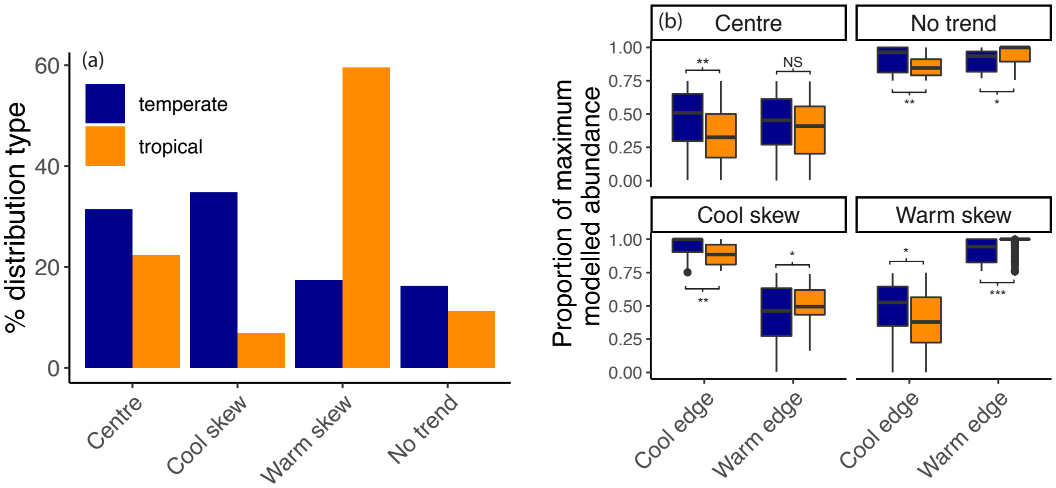

Figure 3.4 (a) Percentage of each distribution type and (b) associated decline in relative abundance at thermal distribution edges relative to T_{opt} across thermal guilds. Panels in (b) are separated by thermal distribution types and x-axis shows thermal distribution edges.

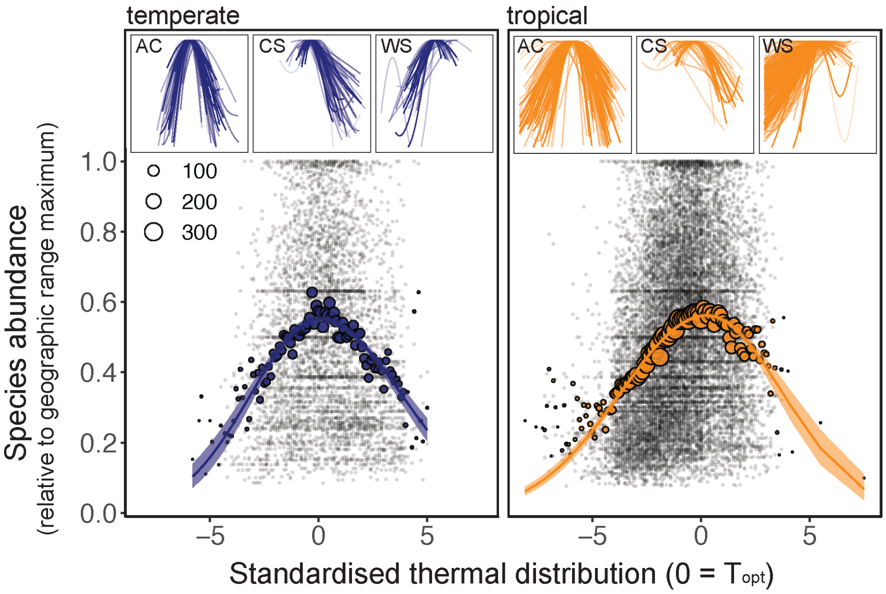

Figure 3.5 Species abundance across thermal distributions for 702 reef fishes on common scales of abundance and temperature. Abundance declines with temperature deviation from T_{opt}, that is, towards thermal distribution edges. The x-axis represents the number of standard deviations from T_{opt} (note the scale on x is standardised within each species range so is not comparable to an absolute temperature value, see Methods for details). Abundance on the y- axis is the local site abundance as proportion of each species' maximum abundance across species' geographic ranges. Small points are individual species' 99th quantile of relative abundance, and large points are mean values across species within a temperature bin. Main panels show Bayesian model fits, fora split-Gaussian distribution, and 95% credible intervals. Panel insets show quantile generalised additive model fits for all 702 species. The split-Gaussian distribution is formed of species' displaying generally abundance-centre (AC) patterns with a relatively even number of cool skew (CS) and warm-skew (WS) species forming the net Gaussian shape that has similar rates of change above and below T_{opt}.

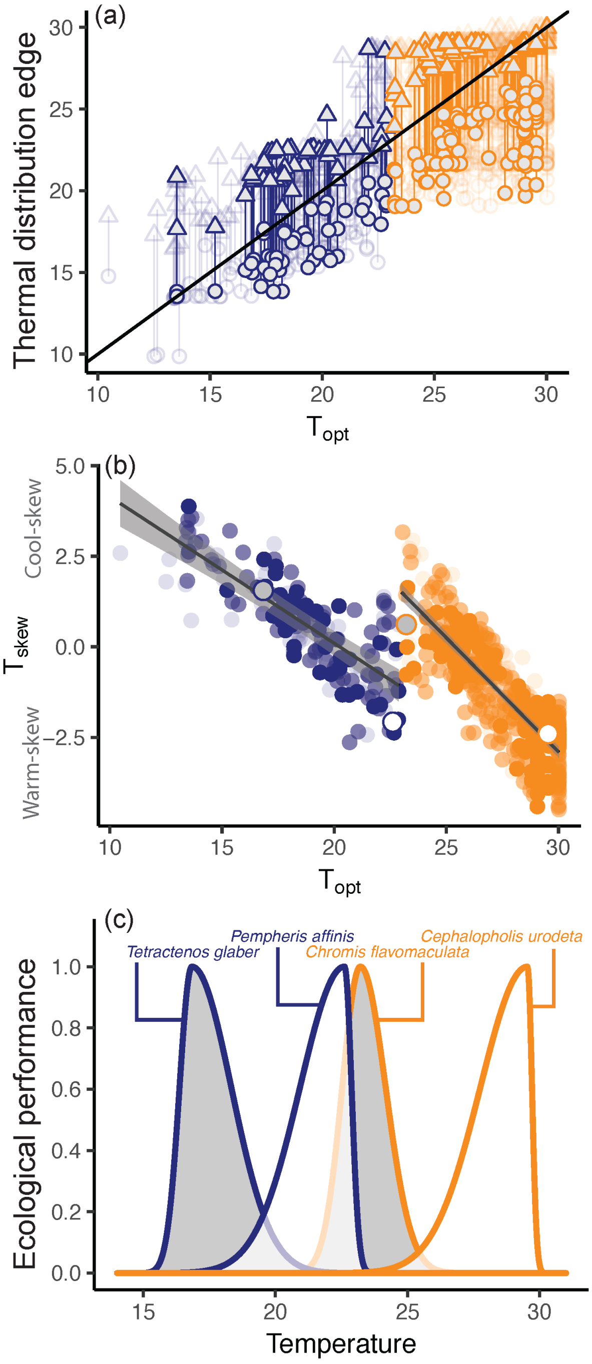

Figure 3.6 Thermal guilds structure the shape of species' thermal distributions (blue = temperate, orange = tropical). (a) The placement of thermal niche edges (T_{min}, T_{max}) relative to thermal optima (T_{opt}) which together define realised thermal niche shape (T_{skew}). T_{max} and T_{min} show relative invariance across T_{opt} within each thermal guild but T_{opt} does vary between species in each guild. Triangles represent upper thermal distribution edges, circles represent lower thermal distribution edges. (b) Shows the negative relationship between T_{opt} and T_{skew} which is a consequence of the invariance of thermal distribution edges in comparison with variable T_{opt} shown in (a). Coloured points in (b) represent partial residuals of species parameter values, excluding the effects of phylogeny and habitat association (coral and algal). Fitted lines are the predicted relationships from a generalised linear mixed-effects models with associated 95% confidence intervals (see Appendix 3: Table S4). Shading indicates confidence scores for species. Large grey or white points represent the species shown as examples in (c). (c) Extreme thermal distribution shapes defined by split-Gaussian functions, and their associated skew, for temperate and tropical guilds at thermal guild edges. Whilst some species within each guild can have high ecological performance at the thermal guild 'barrier' (~ 23°C) in both guilds, some species segregate strongly at this barrier and do not occur in both guilds.

curves at T_{opt}. Species' abundance at T_{opt} was only 55-56% maximum abundance observed across a species' range (Figure 3.5).

3.4.3 Quantifying structure in the thermal-abundance distribution shape

Species within thermal guilds generally shared thermal distribution edges (Figure 3.6a), but the positions of the peak and the degree of skew were more variable (Figure 3.6b). A slight negative skew existed when averaged across all species (i.e., warm-skew, median T_{skew}=-0.98, IQR=2.32). T_{opt} and T_{skew} were significantly negatively related (Figure 3.6b). This was stronger for tropical (β=-0.63±0.02) than temperate guilds (β=-0.40±0.04; Z=-5.40, p<0.001), thus the transition from cool- to warm-skew occurs more rapidly along the thermal gradient among tropical species. Contrasting patterns of skew in temperate and tropical species in subtropical regions means that species from different guilds can share a similar T_{opt}, despite having different thermal distribution edges (e.g., Figure 3.6c). Model fits were not improved by including taxonomic structure as a proxy for shared evolutionary histories for tropical or temperate species. Results were also robust to inclusion of only 'high-confidence' species (Appendix 3: Table S5) and were similar when I used T_{min} and T_{max} derived from species' distribution models or seasonal extremes (Appendix 3: Table S4, Figure S11, S12).

Species' T_{opt} and habitat associations both independently contributed to the shape of T_{skew}. Within the sub-tropical transition zone, species that were strongly associated with coral or algal habitats were most strongly skewed, declining in abundance in temperatures where favoured habitats become unavailable (Figure 3.7). In contrast, species weakly associated with either habitat type retained abundance across this habitat transition thus having less skewed thermal distributions when optima are located in sub-tropical temperatures.

3.5 Discussion

Species' abundances are structured along environmental temperature gradients in a pattern consistent with the abundant centre hypothesis. Multiple lines of evidence support this result, first, a peak in maximum abundance occurs in most species. Second, local maximum abundances decline towards each thermal-distribution edge at a similar rate. Third, for species that have thermal niche edges available in geographic space (i.e. ranges not constrained by the edges of continents or the warmest seas) almost all show some decline in abundance at thermal distribution edges (97%). Whilst many species display a peak in abundance, truncation of the warm edge for tropical species combined with the fact that there are many more tropical species, leads to a high overall frequency of species displaying warm-skewed realised abundance-distributions (i.e., in my categorical assessment, section 3.3.2).

I provide arguably the most robust assessment of patterns of abundance across an environmental gradient to date (but see Santini *et al.* 2018). These findings contrast previous studies that largely focus on terrestrial or intertidal species (Sagarin & Gaines, 2002; Dallas *et al.*, 2017) by finding that species' abundances frequently display realised niche optima, and that abundance declines at a similar rate towards each niche edge – I interpret this as a signal of a net abundant-centre pattern. This contrast suggests the effect of climate on ecological performance may be obscured on land by small-scale processes and factors such as human alterations to habitat availability (i.e., land-use change) and microclimate variability. Shallow reef fishes could be considered an ideal 'model' taxon, given the relatively low thermal heterogeneity and high spatial auto-correlation of temperature in sub-tidal marine systems (Steele & Henderson, 1994), leading to a reduced capacity to behaviourally thermoregulate (but see Chase *et al.* 2018). Furthermore, terrestrial species which strongly regulate body temperatures – either physiologically (hibernation, endothermy) or behaviourally (burrowing, seeking shade) – may be less likely to show reduced performance at sub-optimal temperatures.

Species in each thermal guild have aligned thermal distribution edges (Stuart-Smith *et al.*, 2015, 2017). Thus, if all species displayed thermal-abundance distribution shapes consistent with the abundant-centre hypothesis, we would observe a local 'build-up' in total community abundance at the centre of each thermal guild (i.e., ~17°C and ~26°C). However, I found that ecological optima were generally offset relative to each other along the environmental temperature gradient – a pattern I call 'thermal complementarity' (Figure 3.6). Moving north-to-south along coastlines within any given region, there is turnover in the species that are living at their optimal temperature for achieving maximal abundance. Environmental or ecological mechanisms may regulate which species reach their peak abundance along thermal gradients. The mechanisms of this ecological temperature optimisation and segregation require further investigation but could include physiological adaptations to temperature; species interactions partitioning the thermal niche (Attrill & Power, 2004; Paterson & Blouin-Demers, 2017); habitat distributions within niche space; or recruitment biases towards particular temperatures or latitudes.

Where thermal guilds turn over rapidly in subtropical regions, the switch in which species are most abundant at any particular site appears to relate to habitat, which transitions from coral to rocky reefs at higher latitudes, but may be dominated by either habitat at

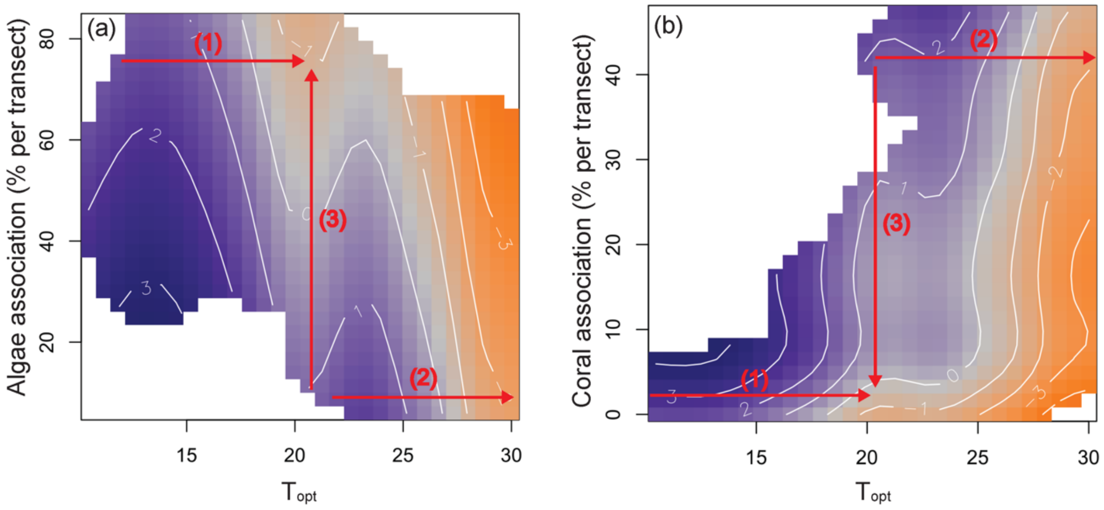

Figure 3.7 Contour plots showing the response of T_{skew} to T_{opt} and species habitat associations: (a) macroalgae, (b) coral. Shading represents cool (blue) to warm (orange) skewed distributions for a given habitat association and thermal optimum. Gradients in T_{skew} occur not only with increasing T_{opt} (arrow 1 and 2 – as in Figure 3.4b), but also in relation to the local cover of macroalgae and coral at survey sites due to species association with particular habitats (arrow 3). The transition from temperate to tropical fish species is also characterised by a transition from macroalgal to coral habitats, but within this subtropical transition zone T_{skew} varies sharply with habitat association.

subtropical sites. Seasonal temperatures may also prove too extreme for tropical and temperate species living close to their cool and warm thermal limits, respectively (Figueira *et al.*, 2009). Further work is needed to evaluate the underlying mechanisms of thermal complementarity alongside the correlative approach used here. Natural experiments in which species' distributions change (range shifts, invasive species, or exploitation), or experimental transplantations (Lee-Yaw *et al.*, 2016) provide opportunities to study the influence of species interactions on ecological performance, and shifts in optima, with altered community structure (Edelist *et al.*, 2013).

The different patterns in the skew of the thermal distribution on either side of ~23°C are not observed in the critical limits for individual performance from laboratory studies (Appendix 3: Figure S9). Thus, measures of performance for individuals, populations and species may display different responses to temperature, leading to mismatches in predicted responses to temperature change across biological and ecological scales. Always inferring biotic change from laboratory-based estimates of 'performance' could induce systematic biases in predictions of biodiversity change in a warmer world – species never occur in isolation, nor do constant environmental conditions occur in nature. An ensemble of predictive theories and data integration are likely needed from different fields (Sinclair *et al.*, 2016).

Beyond subtropical climates, abundance distributions for tropical species were frequently warm-skewed, but temperate species more frequently displayed cool-skewed or abundant-centre patterns. The distributions of the warmest-affinity tropical species are truncated at their warm thermal distribution edge by the maximum temperatures observed in the oceans. Likewise, the geographic availability of land in southern latitudes may also increase the higher frequency of the cool-skewed distributions in temperate species. These biogeographic factors aside, studies of metabolic performance report that low-latitude reef fishes show optimal temperatures near to upper thermal limits, and can rapidly lose function with even a small increase in temperature (Rummer *et al.*, 2014). Fundamental thermal niches indicate tropical species across multiple taxa live nearest their upper thermal limit – i.e., the 'hotter is better' hypothesis – thus the patterns observed are unlikely to result from a biogeographic boundary effect alone (Deutsch *et al.*, 2008; Angilletta *et al.*, 2010; Morley *et al.*, 2012). I explicitly accounted for the possibility of truncations to thermal-abundance distributions by only analysing species with absences beyond observed range edges, and through trialling exclusion of species with a T_{opt} > median T_{opt} of all tropical species, and the results remained qualitatively unchanged (Appendix 3: Tables S4, S5).

The observational and coarse-scale nature of my analyses, correlating mean temperature to ecological performance, cannot perfectly exclude other factors influencing ecological performance. For example, I overlook fine-scale variability in the temperatures experienced by reef fishes which could yield greater understanding of the links between small-scale temperature variation and ecological performance (e.g., Payne *et al.* 2016). I focus on shallow-water species, but it is possible that abundance at warm-range limits is underestimated if species can occupy deeper and cooler reefs (Bates *et al.*, 2015a). However, shallow and deeper (i.e., mesophotic) reefs are compositionally distinct systems, and so the capacity for deepening at warm range limits may be limited (Rocha *et al.*, 2018) – such a pattern would still be consistent with the idea that warmer seas reduce species' maximum abundance potential in shallow-water ecosystems. In addition, I study a thermal gradient with a correlated transition in dominance from coral to macroalgal cover on reefs (as discussed above; Appendix 3: Figure S10). Although observational analyses are unable to identify temperature as a direct mechanism, my multiple regressions determine that the partial influence of species thermal optima on skew is statistically significant even when correlated habitat associations are considered (Figure 3.6, Appendix 3: Table S4, S5).

The relationship between temperature and maximum abundance suggests at least partial predictability of species-level maximum abundance response to future temperature changes (Booth *et al.*, 2018), and the opportunity to predict changes in maximum abundance across species ranges (Lenoir & Svenning, 2013; Martinez-Gutierrez *et al.*, 2018). Such approaches add to estimates of biodiversity change in response to warming that are generally based on changes in occupancy probabilities – changes in abundance are an important component of temperature-driven biodiversity change, as well as changes in ecosystem function and services (Waldock *et al.* 2018; Chapter 2). For example, a change in the number and proportion of individuals within a community comprises a key mechanism whereby biodiversity contributes to ecosystem functions (Winfree *et al.*, 2015), and the impact of non-native and invasive species is tightly linked to abundance (Sofaer *et al.*, 2018). In addition, the yield of fisheries depends on the number of individuals in local populations, and the success of marine management is usefully measured by an increase in number of individuals contributing to community biomass (Edgar *et al.*, 2014). Consideration of species' thermal-abundance distributions when designating protected areas should enhance biodiversity conservation with climate warming by anticipating, and planning for, species' abundance increases and declines (rather than just presence) inside protected areas (Fredston-Hermann *et al.*, 2018). These examples implicate the importance of monitoring species' abundance and quantifying thermal-abundance distribution shapes to better predict and manage shifting biodiversity in a warming ocean with greater temperature extremes.

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Chapter 4 Response diversity of reef fish functional groups in a thermally-shifted ecosystem

4.1 Abstract

Heatwaves will increase in frequency with climate warming. For coral-reef fishes, heatwaves cause a simultaneous shift in ocean temperatures, algal food resources, and coral habitat cover. Particular groups of reef fishes in local assemblages provide important ecosystem functions[1] – e.g., predate coral, bioerode the reef matrix, or consume algae. How these functional groups change in abundance and occurrence with further warming is expected to influence coral reef ecosystems. The diversity of response to environmental change within a functional group affects the resistance of ecosystem functions to change. Patterns in the response diversity of reef fishes at local and regional scales are generally unknown. I quantify the response of 134 reef fishes in 5 functional groups to spatial environmental gradients that characterise temporal changes during heatwave events across the Great Barrier Reef and western Coral Sea. Next, I quantified response diversity as the variation in species' spatial response for each functional group within local assemblages and the regional species pool.

First, I aimed to quantify spatial patterns in response diversity in functional groups that affect benthic habitat structure on the Great Barrier Reef and western Coral Sea. I found response diversity was often spatially homogenous across assemblages for many functional groups. Therefore, movement and dispersal of species between assemblages could potentially maintain local resilience of ecosystem functions after heatwave events. For some functional groups, the response diversity of the regional pool was similar to the response diversity in local assemblages. This similarity in response diversity at multiple scales suggests environmental filtering selects for a resilient local assemblage. These potentially novel mechanisms of local resilience, through regional patterns of spatial response diversity, warrant further investigation.

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[1] I refer to these as 'functional groups' throughout as I am interested in their role in altering benthic habitat structure rather than their trophic position per se, see section 5.2 for further details.

Second, I aimed to simulate occupancy responses to multiple environmental changes. I determine the relative effect of each environmental change, on average, for each functional group within local assemblages. I used realistic environmental changes monitored during the 2015-2016 summer heatwave event that resulted in coral bleaching. Simulated warming increased occupancy rates for all functional groups. Coral loss negatively affected corallivores and excavators (i.e., if bleaching occurs). Surprisingly, no groups were very sensitive to changes in algae cover, perhaps due to high levels of response diversity in these assemblages.

Overall, I present a holistic view of response diversity using standardised metrics amongst functional groups for the local assemblages within a regional species pool. These broad-scale insights of how functional groups, and their ecosystem functions, may persist during environmental change provides specific hypotheses for more targeted approaches to challenge.

4.2 Introduction

Climate change is reorganising coral-reef ecosystems. Recently, focus has shifted from the ecological effects of long-term warming to the importance of ‘heatwave’ events (Stuart-Smith *et al.*, 2018; Smale *et al.*, 2019). The natural disturbance regimes on coral reefs are likely to be disrupted by climate warming. (Halford *et al.*, 2004; De’ath *et al.*, 2012; Adam *et al.*, 2014). For example, over the past 30 years coral cover on the Great Barrier Reef has halved due to increasing frequency of disturbances; heatwaves will increase in the frequency of disturbed reef states (De’ath *et al.*, 2012). Multiple ecosystem functions and ecosystem services are contributed by reef fishes. Therefore, quantifying the resilience of fish assemblages to changing reef environments with warming is important (Bellwood *et al.*, 2004; McClanahan *et al.*, 2014).

Herbivorous and corallivorous fish may play a particularly important role in mitigating climate-change impacts on coral reefs (Edwards *et al.*, 2011; Cheal *et al.*, 2012). For example, increasing herbivore diversity reduces algae cover with a subsequent increase in coral recruitment because complementary modes of herbivory exist (Burkepile & Hay, 2008, 2011; Rasher *et al.*, 2013; Mumby *et al.*, 2016; Lefcheck *et al.*, 2019; but see Bruno *et al.*, 2019). Single species can also ‘over-contribute’ to particular forms of herbivory (Hoey & Bellwood, 2009). Herbivorous fish may buy time for coral reefs by delaying future coral loss by up to 50 years (Edwards *et al.*, 2011). On the other hand, excavating corallivores can contribute substantially to reef carbonate budgets and may limit reef post-disturbance coral recovery (Perry *et al.*, 2014).

4.2.1 Response diversity

The maintenance of specific functions within communities, such as feeding mode and biogenic habitat modification, depends on species which share the same ecological role (i.e., functional group) having separate responses to environmental changes (i.e., response diversity; Figure 4.1). If all species in a functional group are vulnerable to the same stressors entire ecological processes may be lost (e.g., bioerosion). On the other hand, if species have different responses to environmental drivers, the role of a functional group within a system might be protected. The initial diversity of species responses to multiple stressors (i.e., warming and biogenic habitat shifts) may influence the effect of environmental change on ecosystem functioning (Elmqvist *et al.*, 2003; Nyström, 2009; Laliberté *et al.*, 2010; Mori *et al.*, 2013; Garcia *et al.*, 2018). Therefore, a diversity of species responses is expected to provide resistance, i.e., a slower response, in changing ecosystem functions provided by functional groups (Figure 4.1; resistance forms an element of overall resilience; Holling, 1973). Response diversity may be particularly important when functional groups have only a few species providing a function – where species losses cannot be replaced by other species (i.e., no functional redundancy). Coral reef fishes that excavate the reef matrix, providing a bioerosion reef ecosystem function, are vulnerable in this sense (Bellwood *et al.*, 2003).

The response diversity of functional groups has been examined most frequently across agricultural gradients in terrestrial (Laliberté *et al.*, 2010; Stavert *et al.*, 2017) and freshwater systems (Moore & Olden, 2017). Declines in ecosystem function are buffered by response diversity. For example, land-use change causes declines in the nutrient excretion of stream-fish assemblages, but these declines would be 30% lower if assemblages exhibited no response diversity (Moore & Olden, 2017). Response diversity has been investigated indirectly on coral reef ecosystems, assuming relationships between body size and the environmental scale of an organisms response; herbivore biomass was retained during climate disturbances when response diversity was higher (Nash *et al.*, 2016). In benthic marine ecosystems, predatory functions resist change during climate warming by species having different thermal affinities (Selden *et al.*, 2018). In fisheries, where yield is undermined by temperature variability, thermal niche diversity helps to stabilised yield (Dee *et al.*, 2016). Similar mechanisms promoting resistance to climate warming may be present in coral-reef fishes which have complementary thermal abundance optima between different species (Stuart-Smith *et al.*, 2017; Waldock *et al.*, 2019; see Chapter 3) but the diversity of responses to multiple stressors in different functional groups remains unquantified.

4.2.2 Disentangling simultaneous temperature effects

Alongside response diversity, the direction (i.e., positive or negative effects) and magnitude (i.e., strong or weak effects) of responses to heatwave events are important to consider. Within a functional group species may all respond in the same direction to one stressor, and the opposite direction to another stressor. In addition, different functional groups may respond in different directions to the same stressor. Furthermore, some stressors may be important for one functional group but not another. For example, corallivorous fish may respond negatively to coral decline, and vice versa in herbivores, but both groups may benefit from increased performance in warmer ocean temperatures (e.g., swim speed and digestion rates may increase via ‘hotter-is-better’ principle; Angilletta *et al.*, 2010).

Co-occurring environmental changes influence reef fish assemblage dynamics but at present the observed net effects are difficult to separate (Wilson *et al.*, 2006). These simultaneous effects vary in magnitude and are complicated by the varying time-periods over which changes occur. For example, changes to reef structural complexity after heatwaves can be slow to decline, and coral-reef can recover if disturbances are intermittent (Halford *et al.*, 2004; De’ath *et al.*, 2012). The short-term negative effect of warming and coral bleaching on fish biomass and abundance can be minimal (Adam *et al.*, 2014; Richardson *et al.*, 2018; Stuart-Smith *et al.*, 2018; Wismer *et al.*, 2019). Lower trophic-level fishes can benefit from warming because degraded reefs have more available resources (Rogers *et al.*, 2018). Warmer temperatures also increase the rates at which low-trophic resources are digested in some herbivorous groups which increases net energy uptake in warmer waters (Floeter *et al.*, 2005; Smith, 2008; Bruno *et al.*, 2015; Heenan *et al.*, 2016; Rogers *et al.*, 2018). In the longer term, heatwaves decrease live-coral cover and increase algae cover, leading to a decline in reef structural complexity (Graham *et al.*, 2006; Bruno *et al.*, 2009). Once the structural complexity of the reef is compromised more consistent declines in fish abundance are observed (Wilson *et al.*, 2006; Pratchett *et al.*, 2008, 2011, 2018), but some species can benefit from decreased structural complexity (Emslie *et al.*, 2014). The fewer fishes that are relatively unaffected by heatwaves and coral bleaching represent a functionally homogenised assemblage (Richardson *et al.*, 2018).

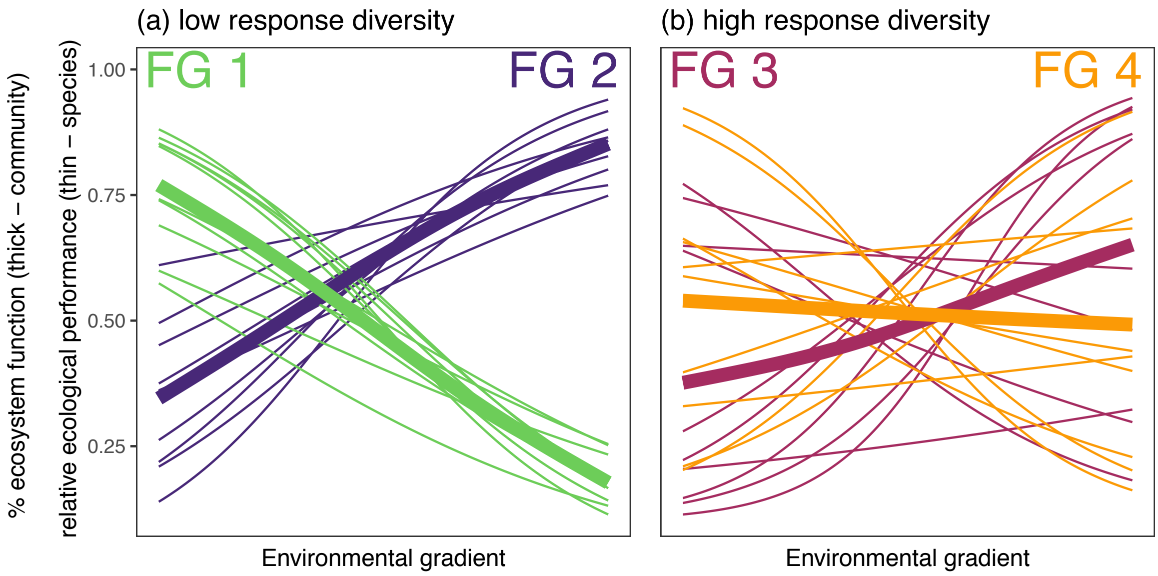

Figure 4.1 Conceptual model of response diversity, response magnitude, and response direction for 4 hypothetical functional groups (FG). Thin lines represent species-specific responses to environmental gradients in terms of occupancy, abundance or physiological performance, thick lines represent average % ecosystem functioning across all species. (a) low response diversity can have negative (FG1) or positive response direction (FG2), within these functional groups response magnitude is always large and all species have the same response direction. (b) high response diversity leads to more stable ecosystem functioning for FG3 and FG4 despite some species have a strong magnitude of response. Note that response diversity conceptualised here is a single response but I use functional dispersion of multiple responses as a measure of response diversity.

4.2.3 Spatial approach and aims

A spatial approach may help in estimating response diversity, and in disentangling responses to multiple environmental changes, by overcoming limitations associated with temporal and experimental approaches. Uncertainties currently exist in how different functional groups respond to multiple stressors (Harborne *et al.*, 2016) and transitionary reef phases (Halford *et al.*, 2004; Rogers *et al.*, 2018). Fishes dynamics over short-time periods are most frequently considered (i.e., <10 year, Wilson *et al.*, 2006; but see Graham *et al.*, 2007) but disentangling complex co-occurring effects from temporal observations is problematic. For example, lag-effects and population stochasticity result in short-term responses that do not necessarily represent longer-term dynamics (Wilson *et al.*, 2006; McClanahan *et al.*, 2007). Whilst experiments may help disentangle the effects of multiple environmental changes, multi-factorial designs are logistically challenging and rarely performed for whole-assemblages of mobile species (Gunderson *et al.*, 2016).

Here, I infer species and assemblage responses to heatwave events using spatial gradients in temperature, coral cover, and algae cover – the environmental variables that shift during heatwaves. Using spatial data has two major benefits. First, spatial data have many more observations than temporal comparisons. As such, we can more easily detect the statistical effects necessary for quantifying multiple species responses to for response diversity, and in disentangling heatwave effects. Second, because a diversity reef states exist, from coral- to algal-dominated, functional group resistance to heatwaves can be inferred from spatial patterns in occurrence (Pickett, 1989; Blois *et al.*, 2013; but see Damgaard, 2019). While this approach has short-comings (e.g., assuming stationarity, population equilibrium, and equilibrium of realised and fundamental niches; Damgaard, 2019), it provides a different perspective to short-term temporal surveys.

I present the largest analysis of response diversity of reef fish functional groups to date. I examine over 250 local assemblages for 134 species in five functional groups that contribute to processes affecting benthic habitat structure and coral reef resilience to heatwaves. I first aim to describe spatial patterns in the response diversity of local assemblages. I examine whether functional groups with high response diversity in the regional species pools also have high response diversity in local assemblages. Second, I aim to examine how each functional group differs in response direction and magnitude to each environmental stressor during simulated heatwave events. I predict that algal farmers, browsing herbivores, and scraping herbivores will show systematic positive responses to increased algal cover; that corallivores and excavators will decline in occupancy with decreased coral cover; but that, on average, all functional groups will benefit from warmer waters (i.e., hotter-is-better hypothesis).

4.3 Methods and materials

4.3.1 Data

The Reef Life Survey (RLS) database provided species occurrence records for all analyses (accessed May 2017). RLS is a visual census of shallow-water reef fish assemblages; survey participants followed strict data-quality controls. Methods are detailed elsewhere and are available from published sources (Edgar & Stuart-Smith 2014, www.reeflifesurvey.com). In short, RLS surveys were undertaken as two 500m^2 blocks either side of a 50m long transects. I defined presence at a transect scale if a species was present on either block. The transect scale is referred to as a ‘survey’ throughout and RLS ‘sites’ are surveys < 200m apart. I only included only adult individuals of non-cryptic species (>40% maximum body length and ‘method-one’ surveys; Froese & Pauly, 2000; Edgar & Stuart-Smith, 2014; Waldock *et al.*, 2019) because juveniles can be strongly influenced by transient events (i.e., spawning, settlement) and cryptic species were small contributors to functional group biomass (just 5% species in the functional groups considered were classified as cryptic).

I filtered the dataset for algal farmer, browsing herbivore, scraping herbivore, excavator and corallivore functional groups. These five categories provided a well-established and simple estimate of the functional contribution of reef fishes (Green & Bellwood, 2009) even though some trophic-level variation exists within each functional groups (Figure 4.2). Each herbivore group interacts with different algae groups but can promote a similar ecosystem functions (i.e., facilitating coral recruitment). Scraping herbivores feed on epilithic and low algae turfs helping reduce colonisation rates and promoting coral recruitment. Algal farmers can be important in coral-algal spatial dynamics. Browsing herbivores crop larger macroalgae preventing coral over-growth and may reverse shifts coral-algae phase shifts (Bellwood *et al.*, 2004; Green & Bellwood, 2009). Excavators contribute to bioerosion of reefs, removing dead coral, by taking deep excavating bites from hard reef substrate (Bellwood *et al.*, 2003; Perry *et al.*, 2014). Corallivores feed directly on coral polyps, affecting coral growth and reproduction which may undermine coral resilience to stressors (Rotjan & Lewis, 2008).

I filtered for species of the five functional groups found on RLS surveys within a bounding box of -30° to -5° latitude and 137° and 160° longitude, encompassing the Great Barrier

Reef and western Coral Sea (GBR-CS), returning 134 species. I obtained RLS occurrence records across the global RLS dataset for these 134 species present on the GBR-CS. I built models for species' global ranges to prevent artificial range truncation which biases estimates of species' responses to environmental gradients (Sánchez-Fernández *et al.*, 2011). I defined absences from a circular buffer with a radius of 2° at a survey. I included all surveys where the species were not observed but were observed elsewhere within this buffer. This buffer is smaller than in Chapter 3 to decrease the sparsity of the community occurrence matrix. This estimate of species' absences overlooks potential observation errors, but is preferable to a pseudo-absence approach. The final dataset included 133,667 presence-absence records for 1820 surveys. I focussed the results on the assemblages within 138 sites (2 surveys per site) across the GBR-CS.

Depth, live coral cover, algae cover and protection management scores were estimated directly during local surveys. Depth was measured as the mean depth contour of transects during surveys (mean = 7.8±5.12). Live coral cover and algae cover were provided from photo-quadrats (PQs) detailed in Cresswell *et al.* (2017). 20 PQs were taken vertically downward per transect every 2.5 meters and were scored using a grid overlay of five points per PQ (100 points per transect, also see Stuart-Smith *et al.*, 2018). Original cover categories were scored into 50 morphological and functional groups. Here All algae (including micro- and macro-algae) categories and all live hard coral categories were summed into % cover per transect for these two groups (as in Stuart-Smith *et al.* 2018). A variety of reef states exist, varying between 75% coral cover to 100% algae cover (Figure 4.3). I used the cumulative protection status scores from Edgar *et al.* (2014), updated in 08/2018, summing the presence of five indicators of high-performing MPA (No take, well Enforced, Old, Large, Isolated) giving a 'NEOLI' score for each site ranging between zero and five. Increasing NEOLI scores indicates increases to reef fish local biomass; a NEOLI score of 3-5 represents a well-functioning marine protected area (Edgar *et al.*, 2014).

I matched site locations to environmental covariates available from the global-scale marine covariate databases. From the Marine Socio-Ecological Covariates dataset (Yeager *et al.*, 2017), I obtained estimates of human population density within a 20km radius, reef area within a 15km radius (Burke et al. 2011), net primary productivity (mg C m^{-2} day^{-1}) and mean wave energy flux (kW m^{-1}) gridded at a resolution of 2.5 arcmin. From bio-ORACLE-v2 (Assis *et al.*, 2018), I obtained surface pH, mean nitrate (mmol m^{-3}) and mean current velocity (m s^{-1}) gridded at a 5 arcmin resolution. I excluded estimates of minimum oxygen concentration and salinity from consideration due to strong covariation with sea-surface temperature. To help reduce the number of parameters in these models,

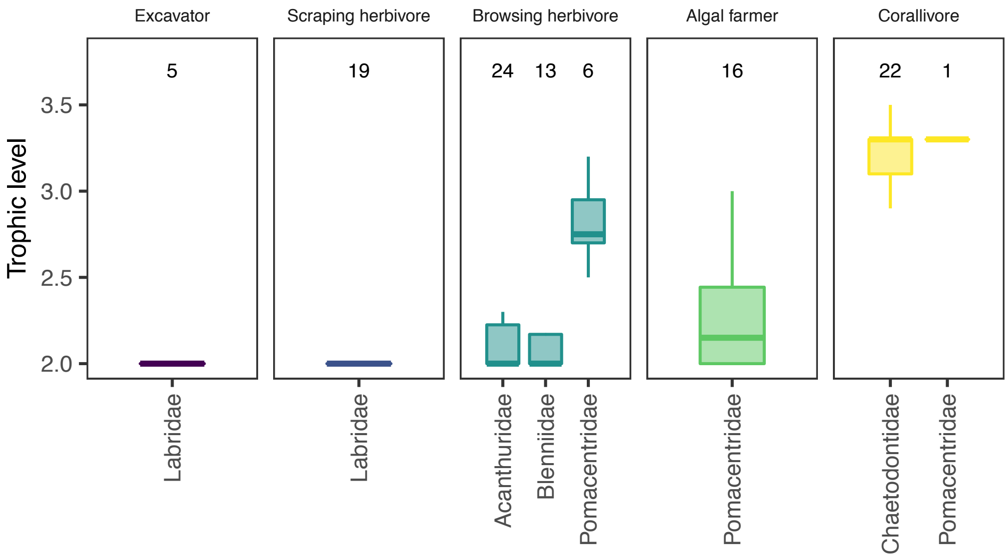

Figure 4.2 Variation in trophic level amongst reef fish functional groups separated by family. Number of species within each functional group and family are indicated above boxplots. Trophic level of 2 indicates feeding on primary produces (i.e., primary consumers) and 3 indicates feeding on primary consumers.

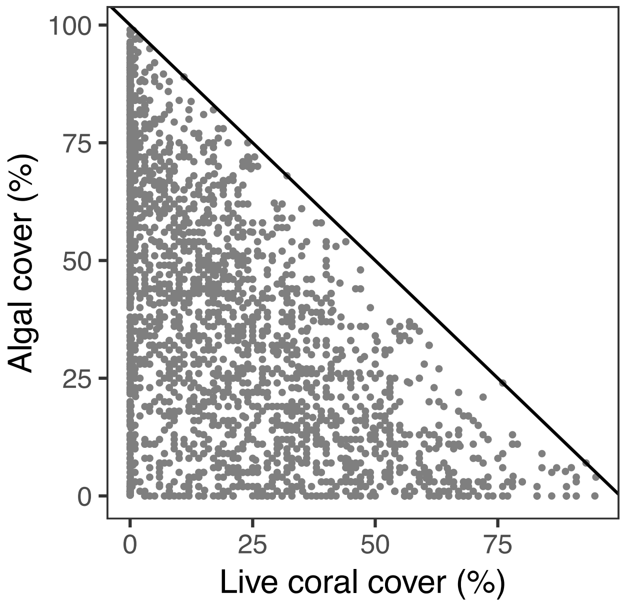

Figure 4.3 Distribution of reef states based on proportions of live-coral and algal cover in the analysis, which varies dramatically. An array of reef-states exists that where coral and algal cover can trade off directly (i.e., the 1:1 line), or alternative low cover of both indicates high cover of bare rock, sand, or soft coral matrix (see classifications in Creswell *et al.* 2017).

I estimated the principal components of these global-scale covariates using robust-principal component analysis (rpca, Hubert 2009). rcpa is tolerant of skewed covariate distributions and outliers. I retained two principal components explaining 80.6% and 14.2% variation in the covariate set. These covariates were not the focus of the heatwave effects, and could not be monitored before and after the heatwave, so reducing to principal components was justified based on the aims of this analysis.

I matched the location of surveys with daily sea surface temperature (SST) calculated to mean SST for one year prior to surveys at a spatial resolution of 3 arcmin (NOAA Coral Reef Watch, 2018). This temporal scale balances the need to quantify the responses of longer-term processes that define species occurrences with capturing heat events such as the 2015-2016 summer heatwave (note that the extremes of this event strongly influence the yearly mean, Figure 4.4).

4.3.2 HMSC modelling to quantify species-specific responses to multiple environmental gradients

I quantified species-specific occupancy responses to environmental variables using the Hierarchical Modelling of Species Communities framework (HMSC; (Ovaskainen & Soininen, 2011; Ovaskainen *et al.*, 2017). From these species-specific responses I estimate response diversity (see 4.3.3). The HMSC framework had three major benefits: i) to quantify parameters describing species-specific responses to covariates, ii) to estimate species-specific responses for rarer or infrequently occurring species with inadequate data to fit independent models (Ovaskainen & Soininen, 2011), iii) to account for the influence of shared local responses to latent environmental variation that might otherwise influence covariate effects (Warton *et al.*, 2015). In addition, combining all species-specific responses into a single framework provided a standardised estimate of variation in species' environmental responses, and therefore capacity to compare regional and local response diversity.

I provide a brief description of my statistical model but full statistical procedures are described elsewhere (Ovaskainen & Soininen, 2011; Ovaskainen *et al.*, 2016a,b, 2017). I modelled the occurrence (*y*, presence-absence) of each species (*j*, where *j=1,...,m*) in each survey (*i*, where *i=1,...,n*) as a probit (generalised) linear model of the form $y_{ij} = probit(L_{ij})$. L_{ij} is the linear predictor that was modelled as the sum of fixed (F) and random (R) effects: $L_{ij} = L_{ij}^{F} + L_{ij}^{R}$. The probit used an inverse-normal link function.

The fixed linear component was estimated from the equation $L_{ij}^{F} = \sum_k x_{ik}\beta_{jk}$.

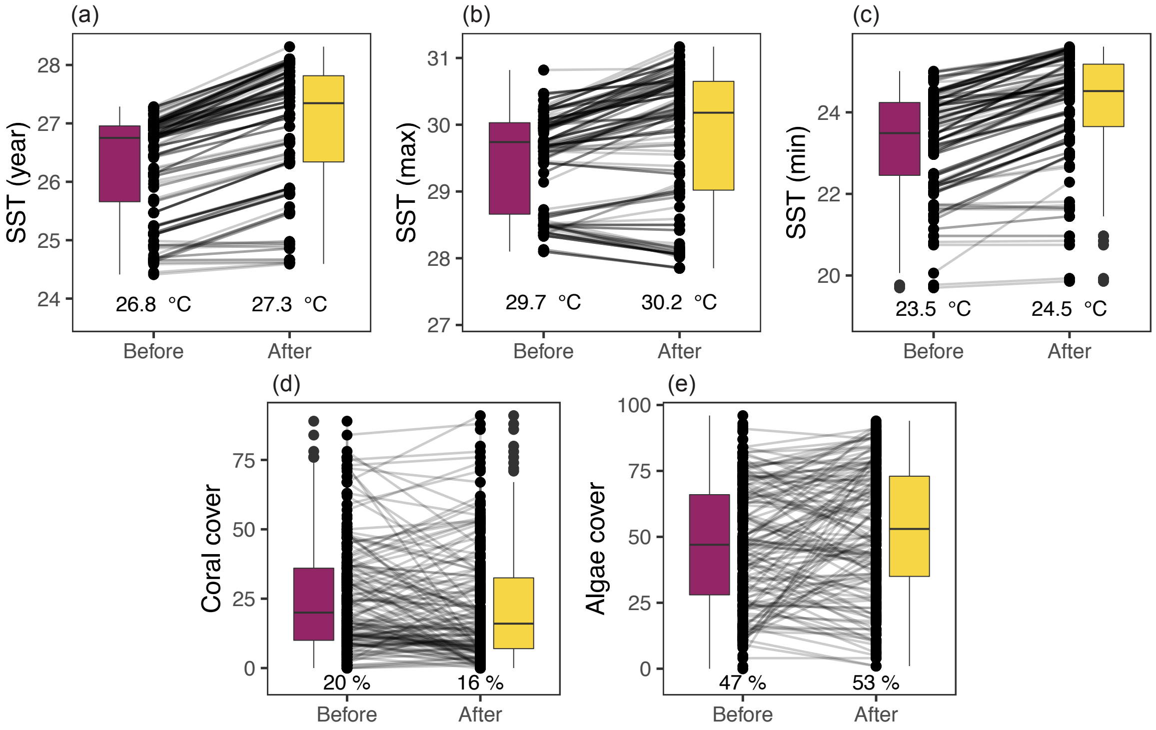

Figure 4.4 Sea-surface temperature (SST) and biogenic habitat changes on the GBR-CS before and after the 2015-2016 heatwave. Yearly mean (a), maximum (b), and minimum (c) daily sea surface temperature (SST) and live-coral (d) and algae cover (e) change. Points represent sites and repeated surveys are linked by lines. Median values in before-after periods are indicated below boxplots. Boxplots show median and interquartile range.

The 7 covariates were represented by *k* (depth, live coral cover, algal cover, NEOLI score, SST, PC1, PC2) and an intercept of 1. In addition to SST, I modelled SST^2 to account for previously described non-linear influence of environmental temperature determining performance of marine ectotherms (Helaouët & Beaugrand, 2009; Payne *et al.*, 2016; Waldock *et al.*, 2019; Chapter 3). x_{ik} denoted the site-specific values of covariate k. β_{jk} denoted the species-specific response to covariate *k*. All covariates were normalised to zero mean and unit variance to make effect sizes comparable and to improve model parameterisation. The focus of this study was in quantifying patterns of β_j which describes the diversity of species' responses to environmental covariates (discussed later). The prior distribution of species-specific covariates adheres to the multivariate normal distribution $\beta_{j.} \sim N(\mu_{j.}, V)$ where $\mu_{j.}$ is the set of environmental responses (i.e., full environmental niche, *k*=1,…,7 for each covariate) of species *j* across '.' environmental covariates. Variation around $\mu_{j.}$ is captured by the variance-covariance matrix *V*. The diagonal elements of *V* measure the amount of variation among the species-specific regression coefficients. The off-diagonal elements of *V* measured the amount of covariation among different species responses to each covariate. While variation in $\mu_{j.}$ can be modelled with phylogenetic distance or species' traits I did not attempt this as it was not the focus of this study and increases model complexity.

The random terms in the model (L^R_{ij}) described the variation in species occurrences and co-occurrences that was not attributed to species-specific responses to covariates. I modelled two hierarchical levels of random effects for each species: transects (i.e., observations) nested in sites ($\varepsilon^S_{S(i)j}$), and sites nested in ecoregions ($\varepsilon^E_{E(i)j}$) as $L^R_{ij} = \varepsilon^S_{S(i)j} + \varepsilon^E_{E(i)j}$, where *S(i)* and *E(i)* indicate the site and ecoregion that survey *i* belongs. These random effects were assumed to be drawn from multivariate normal distributions as $\varepsilon^S_S \sim N(0, \Omega^S)$ and $\varepsilon^E_E \sim N(0, \Omega^E)$ where $\Omega^S \; and \; \Omega^E$ are species-to-species variance-covariance matrix at the site and ecoregion scales. The off-diagonal of these matrices describes whether two species occur less, or more, frequently that expected by chance. This probability was parameterised with a latent-variable approach (mathematical details described in Ovaskainen *et al.* 2016a). In brief, latent variables fitted a linear model to residual variation remaining in the hierarchical-error term. For example, at the site level the random effect was a function of latent variable $\varepsilon^S_{ij} = \sum_k \eta^S_{ik} \lambda^S_{kj}$ where the factor loading λ^R_{kj} described the species-specific effect of latent factor *k* (analogous to a covariate). η^S_{ik} described the latent variable (analogous to an environmental variable) for each survey *i* distributed as $\eta^S_{ik} \sim N(0, 1)$. The latent variables then represent shared species responses to missing covariates. These latent factors could represent species interactions or environmental gradients that are not described in the covariate set. The main benefit using of latent factors here was that fewer parameters describe species associations and enabled a more accurate estimates of co-occurrences for rare species due to shared underlying environmental responses (Warton *et al.*, 2015; Ovaskainen *et al.*, 2016a).

I fitted all models using HMSC-R v2.0 developed under R version 3.3.1 (Norberg *et al.* 2017; Ovaskainen *et al.*, 2017). HMSC uses MCMC Bayesian inference based on Gibbs sampling. I implemented HMSC with default, uninformative, priors (described in Appendix of Ovaskainen *et al.* 2017). I ran models for 5×10^6 iterations with a burn-in period of 2.5×10^6, I thinned chains to give a posterior distribution sample size of 10,000. I ensured chains were converged by testing that i) autocorrelation for a distance of 50 posterior samples and ii) the distribution of Gelman-Rubin statistics, were not significantly different from 0. I performed variance partitioning using the ‘variPart’ function in HMSC-R, described in the Appendix of Ovaskainen *et al.*, (2017), which partitions the variance explained amongst parameters for covariates. I assessed the discriminatory capacity of presences and absences in this model fit. I estimated the area under the receiver-operator curve when predicted into the conditions during the GBR-CS heatwave (i.e., an AUC score, a standard performance measure of binary classifications; McPherson & Jetz, 2007; but see Lobo *et al.*, 2008). This provided a temporal cross validation that provides a more accurate estimate of model performance than leave-one-out or simply a spatial cross validation (e.g., dropping 20% of the dataset).

4.3.3 Patterns in response diversity

I quantified the response diversity of each functional group by measuring the multivariate functional dispersion (FDis) of species-specific responses to SST, SST^2, live coral cover and algal cover (i.e., the coefficients for each of these covariates; Laliberté & Legendre, 2010; Laliberté *et al.*, 2010). I first calculated a Euclidean distance matrix of species-specific responses. I estimated FDis from this distance matrix using the package ‘FD’ (Laliberté & Legendre, 2010). FDis estimated the average distance of species’ response to the functional group centroid in all response space. FDis is insensitive to the number of species (Laliberté & Legendre, 2010). I follow Laliberté *et al.* (2010) in interpreting a decrease FDis as a functional group containing more species that respond similarly to an environmental perturbation. Low FDis can therefore be interpreted as low resistance in the ecosystem functioning, and vice versa. I estimated FDis for each local assemblage at a site level for each functional group, this value was not weighted by relative abundance because rare species can contribute to resilience (Walker *et al.*, 1999). Note that I only estimated FDis for local assemblages where more than one species within a functional group was present. The step may have positively biased response diversity in excavator functional groups because 70% of sites had just one species (all other functional groups had the majority of sites with more than one species per functional group). Estimating response diversity as zero in functional groups with just one species would have strongly confounded local richness and response diversity. Thus, our values of response diversity should be interpreted as the capacity for local response diversity when more than one species in a functional group is present. I also estimated the FDis of all the species within a functional group for the entire regional species pool.

I quantified response direction and response magnitude for each functional group as the mean response of species to SST, SST^2, coral cover and algae cover at each site. The sign and average value indicated the response direction and magnitude (respectively). I mapped response diversity, direction and magnitude by spatially interpolating local assemblage values based on inverse-distance weighting within a buffer with a radius of 0.5°.

4.3.4 Simulating heatwave events on functional group occurrence

I tested for divergent functional group responses to coinciding environmental changes through a series of simulations. First, I simulated the occupancy response of each functional group to temperature, live coral cover and algal cover after the 2015-2016 heatwave event (Figure 4.4, 4.5). I estimated site-level change in SST, live coral and algal cover from matching before-after surveys at 139 sites (each with two surveys) along the GBR-CS from November 2016 to March 2017 (described in full by Stuart-Smith *et al.* 2018). 'Before' surveys were also included in fitting the HMSC model. I simulated occupancy probabilities using the fitted model in 4.3.2 and input covariate values from the before and after surveys. Before survey covariates are as described in 3.2.1. After survey live-coral and algal cover were estimated directly from surveys, SST was calculated as the yearly mean SST from the beginning of the heatwave event (defined as 1st January 2016; Figure 4.5). All other covariates were at the site-level as in 3.2.1. I used the parameters estimated in the HMSC model to predict the species-specific occupancy rates at a site level before and after the heatwave event. I estimated the mean site-level occupancy probability for each functional group using before and after covariates. I estimated the occupancy log-response ratio (LRR) as the mean functional group occurrence probability after the heatwave divided by before the heatwave, I then took the log of this ratio. Positive values indicate occupancy increased after the heatwave. I then fitted multiple regressions for each functional group using LRR as a response variable

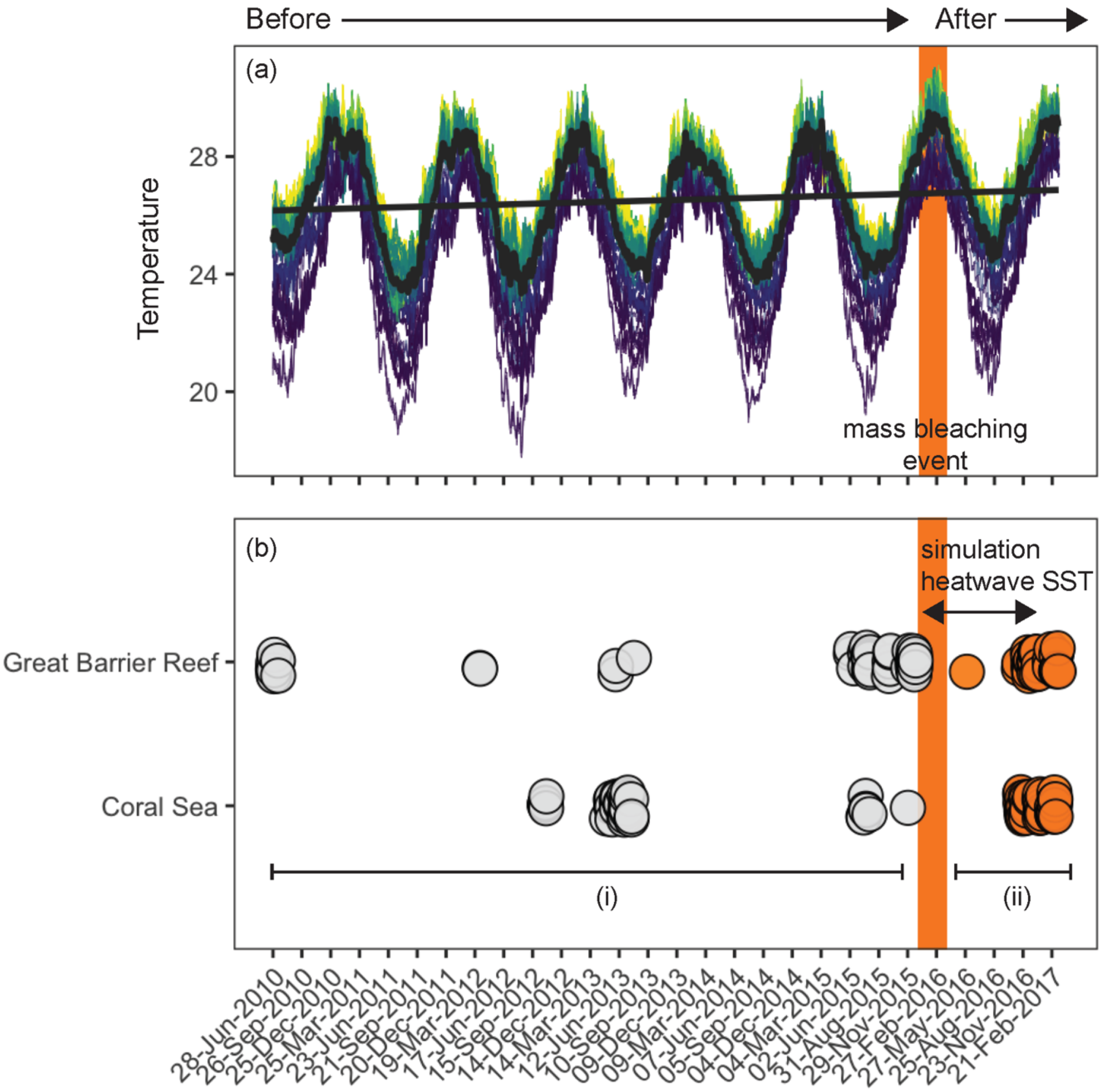

Figure 4.5 Design of study relative to temperature variation and surveys. (a) Daily sea surface temperature obtained from NOAA Coral Reef Watch (2018) for all sites surveyed before and after the 2015-2016 summer heatwave and bleaching event on the GBR-CS. Individual sites are represented by lines and thick black line is mean SST. (b) The temporal distribution of before and after surveys on the GBR-CS where surveys spanning (i) are included in HMSC modelling along with global RLS dataset, and (ii) are after surveys used for cross-validations and heatwave simulations. The overall heatwave event and mass bleaching event is indicated by the orange bar.

and change in temperature, live coral and algal cover as covariates. Covariates were first standardised by subtracting the mean and dividing by the standard deviation. Multiple regressions allowed the independent effect size of each covariate to be estimated for each functional group (Morrissey & Ruxton, 2018).

Finally, I simulated the change in occupancy probabilities, as above, but instead developed scenarios of heatwave events rather than using observed changes in covariates. I isolate changes in one covariate at a time across all sites at the same time, whilst holding all other covariates at their before-heatwave values. I applied warming of 0.2°C, 0.4°C, 0.6°C, 0.8°C, 1°C. I applied live coral cover loss, and algal cover gain, of 10%, 20%, 30%, 40%, 50%. These values match the monitored magnitude of declines in coral and algae cover during heatwave events that result in bleaching and longer-term declines in the quality of reef habitat on the GBR-CS (De'ath *et al.*, 2012; Stuart-Smith *et al.*, 2018). If 'before' surveys had coral or algae cover of <25% or >75% I excluded these from the simulations to prevent change categories less expected (e.g., 5% cover to 0% cover). Because all communities were exposed to the same change in these scenarios, this simulation assessed how the site level variation in species responses alone leads changes in occupancy probabilities (by excluding spatial variation in environmental change). I also examined how LRR varied across latitude by separating change between northern (>-12°), mid (-12° to -19°) and southern (<-19°) latitude reefs.

4.4 Results

4.4.1 Species-specific responses to environmental gradients

Species showed a large amount of variation in their response to different environmental gradients. My results focus on species responses to SST, live coral cover and algal cover, because these variables respond in a predictable direction to heatwave events, but note that additional variation also exists in species responses to other environmental gradients (e.g., PC1, depth, NEOLI). By partitioning the variance amongst explanatory variables, I found that 53% of total variation was explained by SST, coral cover and algae cover combined, but the proportion explained by coral and algae cover was ~ 1% each (Figure 4.6). 22% overall variation in occupancy is attributed to additional covariates and 25% to the effects of latent ‘unobserved’ variables. Overall, model performance was relatively high as indicated by an AUC score of 0.77 when applying the spatial model to the naïve post-heatwave occurrence dataset (i.e., a temporal ‘out-the-bag’ test).

Significant species-level responses to SST, SST^2 and coral cover were more common than to algal cover (Table 4.1). Species varied in the number of significant responses across environmental variables (Figure 4.7). Most species responded positively to SST and negatively to SST^2 indicating that species had a hump-shaped response to SST overall. Species responses to live-coral and algal cover were often non-significant. Those with significant responses more frequently had positive than negative responses to increasing coral cover, even in herbivores. In herbivores, significant responses to algae cover were often positive and negative (Figure 4.7, Table 4.1).

Table 4.1 Summaries of response metrics. The percentage of species in each functional groups in the GBR-CS with negative and positive responses to each environmental change. Response direction is averaged across all species in a functional group for the regional species pool. Response diversity, as functional dispersion (FDis), is estimated for each local assemblage and mean values (sd) shown (1), or for all species in a functional group for the regional species pool (2).

		Scraping herbivore	**Excavator**	**Browsing herbivore**	**Corallivore**	**Algal farmer**
% positive	SST	63.2	60	42	60	56.2
	SST^2	0	0	2.9	12	6.2
	Coral	26.3	60	8.7	48	12.5
	Algae	21.1	0	13	12	12.5
% negative	SST	0	0	4.3	4	18.8
	SST^2	26.3	0	17.4	16	25
	Coral	5.3	0	8.7	4	12.5
	Algae	5.3	0	4.3	24	0
Average response	SST	1 (0.77)	1.1 (0.45)	0.64 (0.79)	0.76 (0.60)	0.75 (1.20)
	SST^2	-0.22 (0.57)	-0.03 (0.32)	-0.18 (0.46)	-0.22 (0.80)	-0.32 (0.60)
	Coral	0.04 (0.11)	0.12 (0.06)	-0.01 (0.10)	0.11 (0.12)	-0.02 (0.14)
	Algae	0.01 (0.12)	0.01 (0.06)	0.01 (0.12)	-0.05 (0.14)	0.01 (0.12)
FDis (1)		0.79 (0.28)	0.17 (0.13)	0.75 (0.16)	0.73 (0.33)	1.02 (0.55)
FDis (2)		0.87	0.42	0.83	0.86	1.20

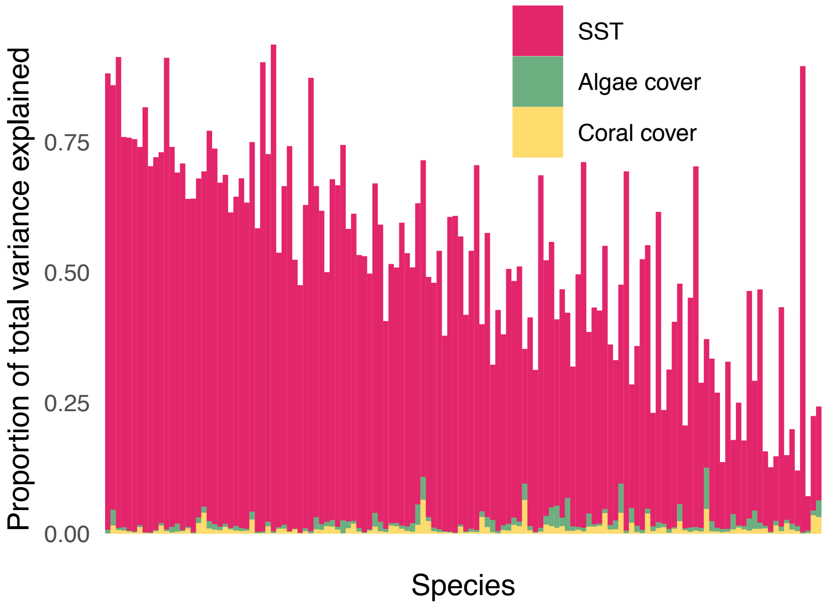

Figure 4.6 Partitioned variance amongst fixed effects. Bars show are the proportion of variance explained by focal variables for each species, ordered by the proportion of variance explained by the linear component of SST.

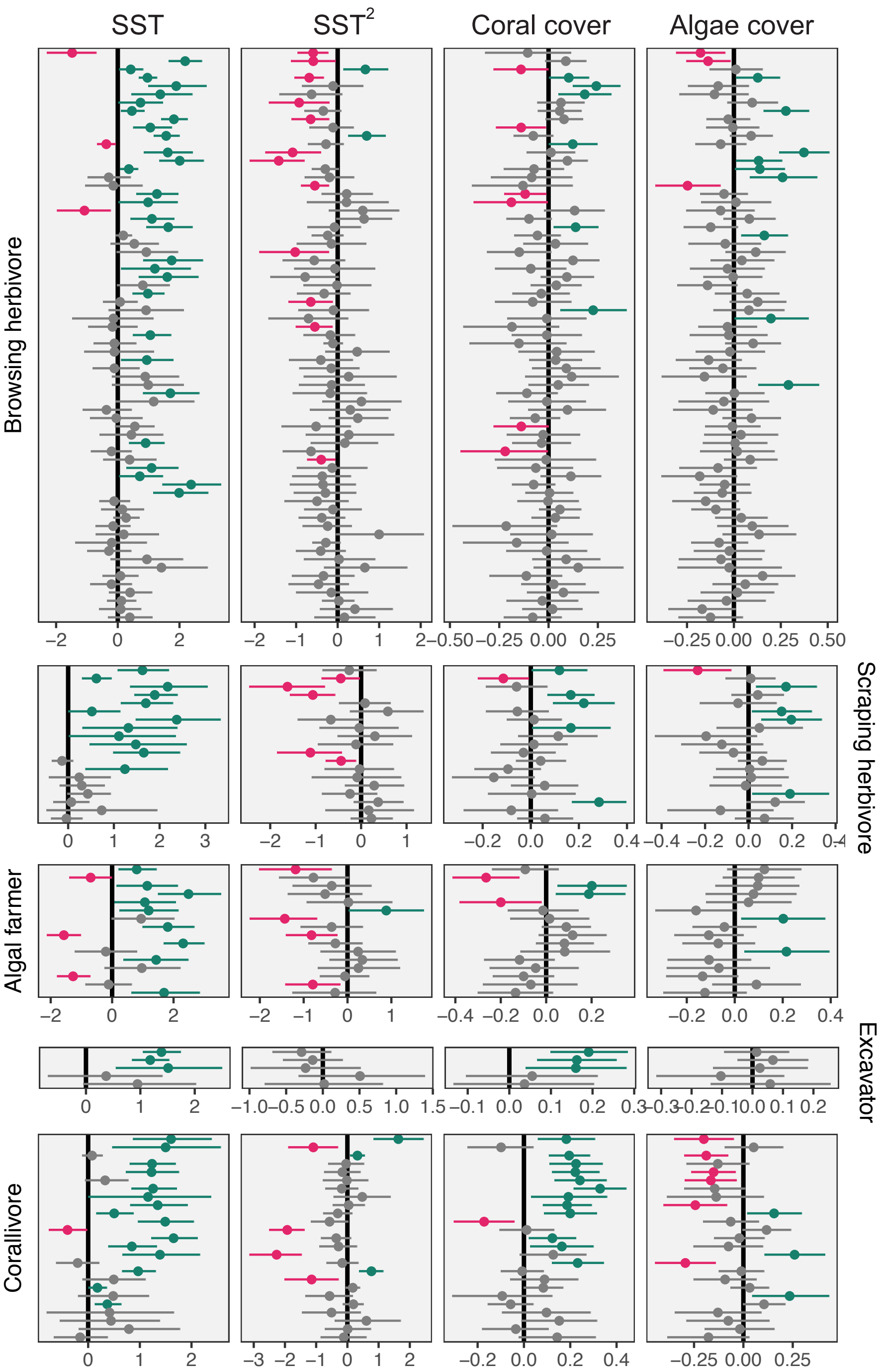

Figure 4.7 Species-specific responses to environmental gradients. Points represent the species-specific mean posterior estimates with ±90% credible intervals for each covariate. Response direction and magnitude are indicated by the x-axis. Species are ordered from top-to-bottom by the number of statistically clear coefficients within each functional group. Green points are show statistically clear positive, and pink points statistically clear negative responses based on 90% credible intervals excluding 0. Grey points have 90% credible intervals overlapping 0 and thus statistically unclear responses to environmental covariates.

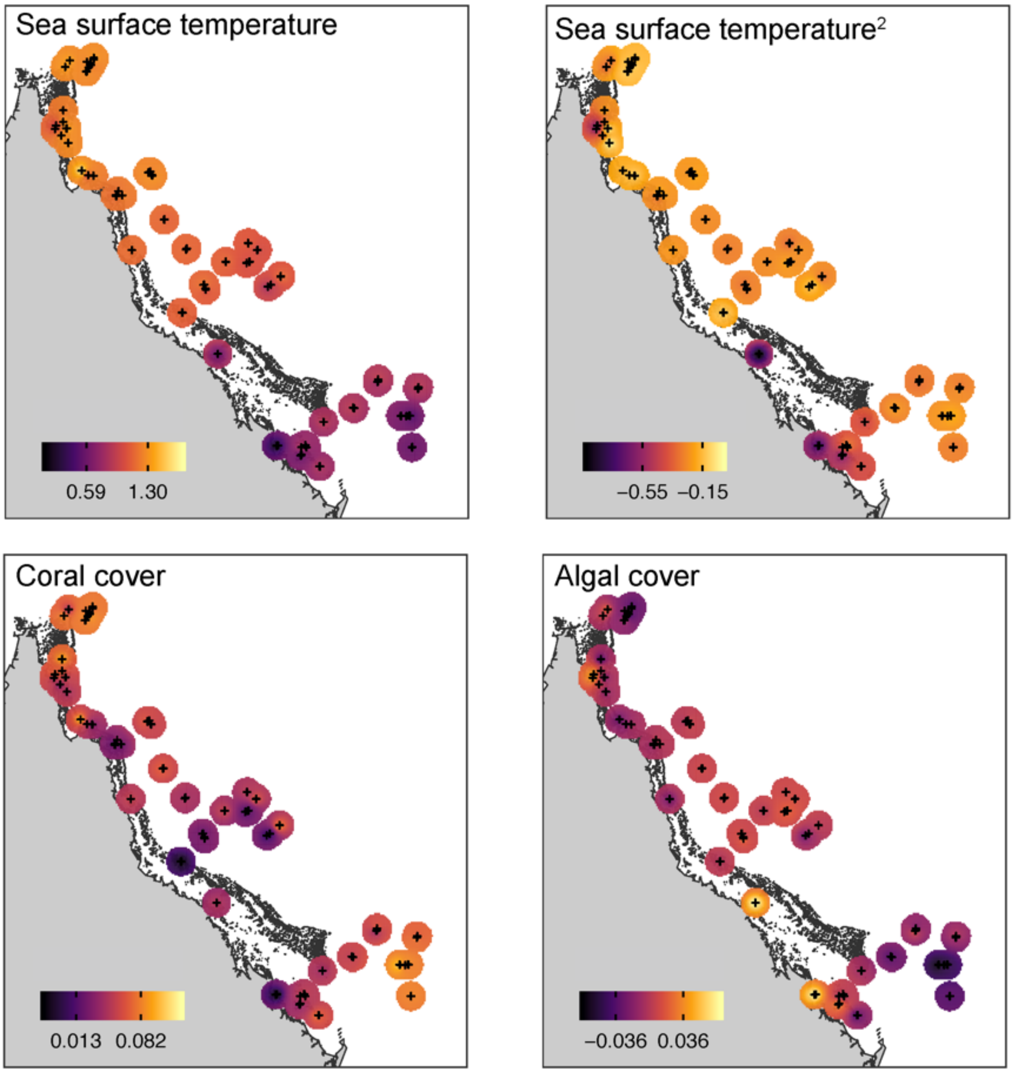

Figure 4.8 Assemblage response direction and magnitude for the GBR-CS. Local assemblage responses are estimated from averaged species-specific coefficient value across all species for each individual survey indicated with plus symbols. Colours indicate values of inverse-distance weighted interpolations based on local surveys. Note that colour scales vary between panels.

4.4.2 Assemblage response direction and magnitude

Assemblage response direction and magnitude show marked patterns of spatial heterogeneity that differed between variables (Figure 4.8). Assemblages in northern GBR-CS consisted of species that showed stronger positive responses to the linear component of SST. The non-linear effect of SST, to induces a humped shaped quadratic effect, was spatially variable and most apparent in the south (Figure 4.8). Assemblage patterns in SST were underpinned by a strong north-south gradient in SST response for all functional groups apart from excavators, which showed consistently strongly positive responses SST to across all surveys (Figure 4.9). Algal farmers showed the strongest north-south gradient in SST response magnitude.

Species responses to coral cover were weakest in the central region of the GBR-CS but stronger, and more positive, at the northern and southern regions (Figure 4.8). Algae cover showed highly heterogeneous responses with only a few sites having very positive species responses that, at least qualitatively, correlates to highly non-linear response of species to SST (Figure 4.8).

4.4.3 Regional and local assemblage response diversity

Regional response diversity (i.e., for all species within a functional group for the GBR-CS) was highest for algal farmers and lowest for excavators, the remaining functional groups had intermediate values (Table 4.1). Response diversity at the local assemblage level was always lower than the response diversity within a regional functional group, indicating some loss of potential resilience as communities are filtered and assemble locally. For browsing herbivores, scraping herbivores and corallivores local response diversity was similar to regional response diversity.

Spatial patterns in local assemblage response diversity varied greatly amongst functional groups (Figure 4.10). Browsing herbivores, corallivores and scraping herbivores exhibited little spatial variation in local assemblage response diversity. Algal farmers had local assemblages with high response diversity in the north and low response diversity in the south-east GBR-CS. Excavators had minimal response diversity across the entire GBR-CS, reflecting the regional faunas limited capacity for response diversity.

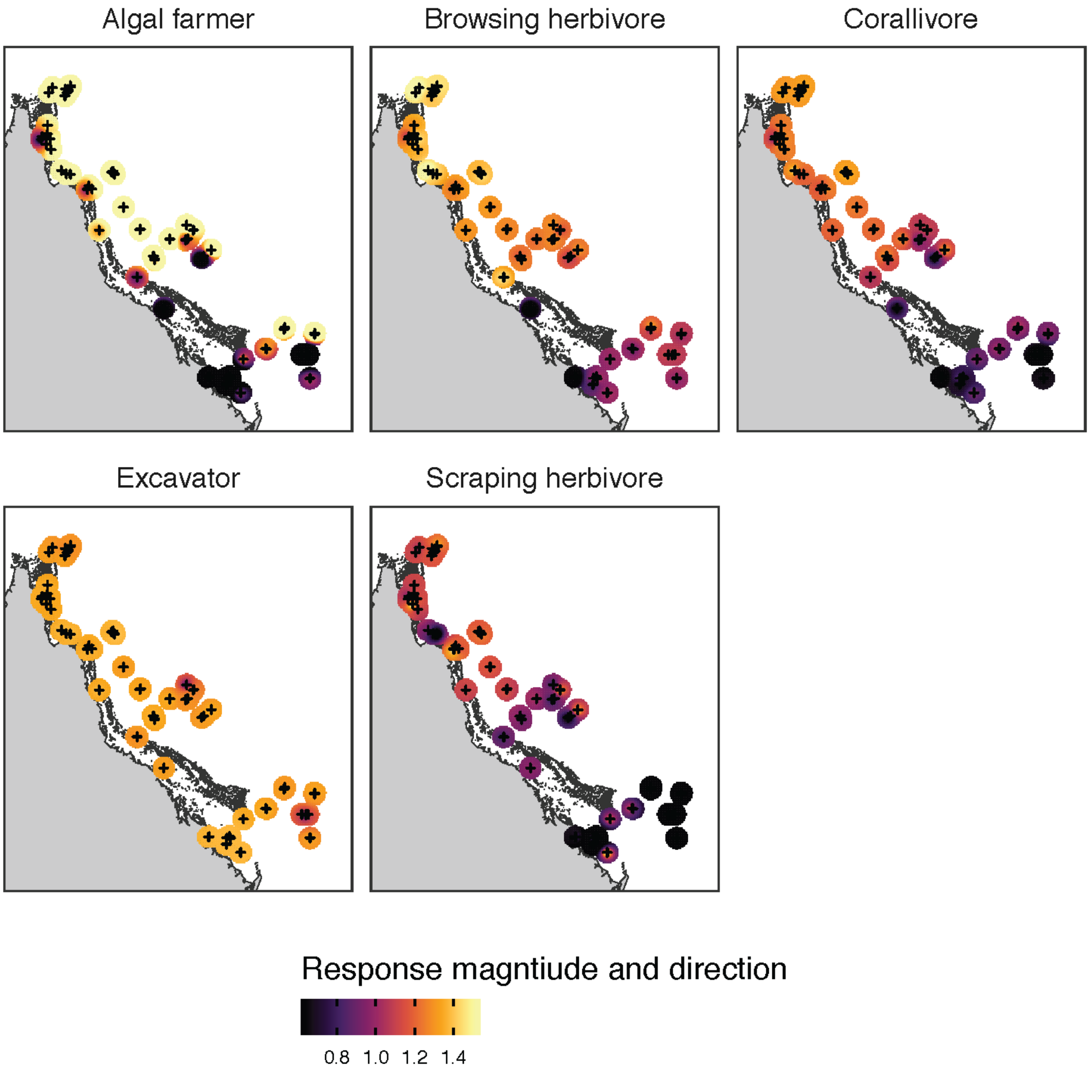

Figure 4.9 Spatial patterns in response direction and magnitude for SST among functional groups. Local assemblage responses are estimated from averaged species-specific coefficient value for sea-surface temperature only across all species for each individual survey indicated with plus symbols. Colour scale is standardised across panels to show comparison of effect size and variation in responses to temperature between functional groups.

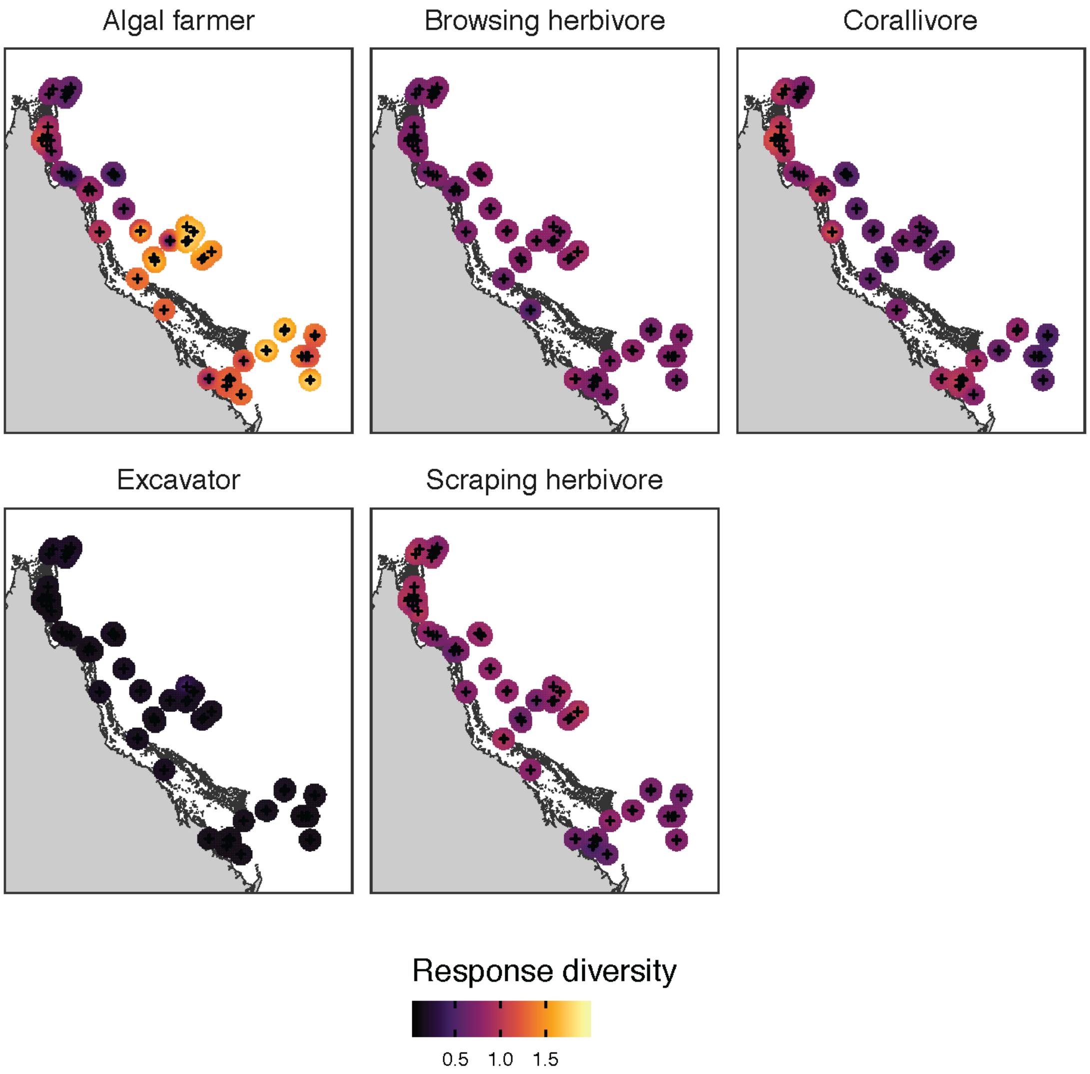

Figure 4.10 Spatial patterns in response diversity (FDis) amongst functional groups. Local assemblage response diversity is calculated from the functional dispersal species-specific coefficient values across all species for each individual survey indicated with plus symbols. Legend colour scale is standardised across panels to show comparison of response diversity between functional groups.

4.4.4 Functional group responses to environmental change

4.4.4.1 Simulating local assemblage responses to environmental scenarios

I found a limited capacity for response diversity to buffer responses to simulated scenarios of environmental change (Figure 4.11). In other words, there were highly consistent responses within each functional group between different local communities to most aspects of environmental change during a heatwave. Here, response diversity would confer resilience to a proportion of local communities if overall occupancy response ratios overlap 0; if no communities overlap 0, then all surveyed local communities in the regional GBR-CS assemblage would show a systematic directional occupancy change. Algal farmers were the only functional group with local communities that exhibit some resilience to all focal environmental changes (i.e., distribution of response-ratios overlaps 0 for all environmental variables).

For some functional groups, responses to multiple environmental changes had counteracting effects. For example, corallivores and excavators show strong positive responses to temperature but a strong negative response to the simultaneous coral loss that also occurred across the GBR-CS (Figure 4.11).

The responses of local communities showed little consistent pattern based on latitude. For example, southern assemblages were often as sensitive as northern assemblages to temperature change (Figure 4.11). Latitude showed inconsistent patterns amongst heatwave stressors too, for example, mid-latitude algal farmers were not sensitive to temperature but were sensitive to coral cover loss.

4.4.4.2 Simulating local assemblage responses to observed heatwave

I found that the environmental shifts during the 2015-2016 summer heatwave and bleaching event had substantial effects on occupancy response-ratios. Changes in temperature and coral cover most strongly influenced LRR (Figure 4.12). The effect of SST change was in magnitude and direction for all functional groups. The loss of coral cover during the heatwave had a negative effect on LRR for corallivores and excavators (Figure 4.12). The effect of heatwave driven increases to algae cover on LRR were generally weak, but had a negative effect on corallivores and a positive effect on scraping herbivores.

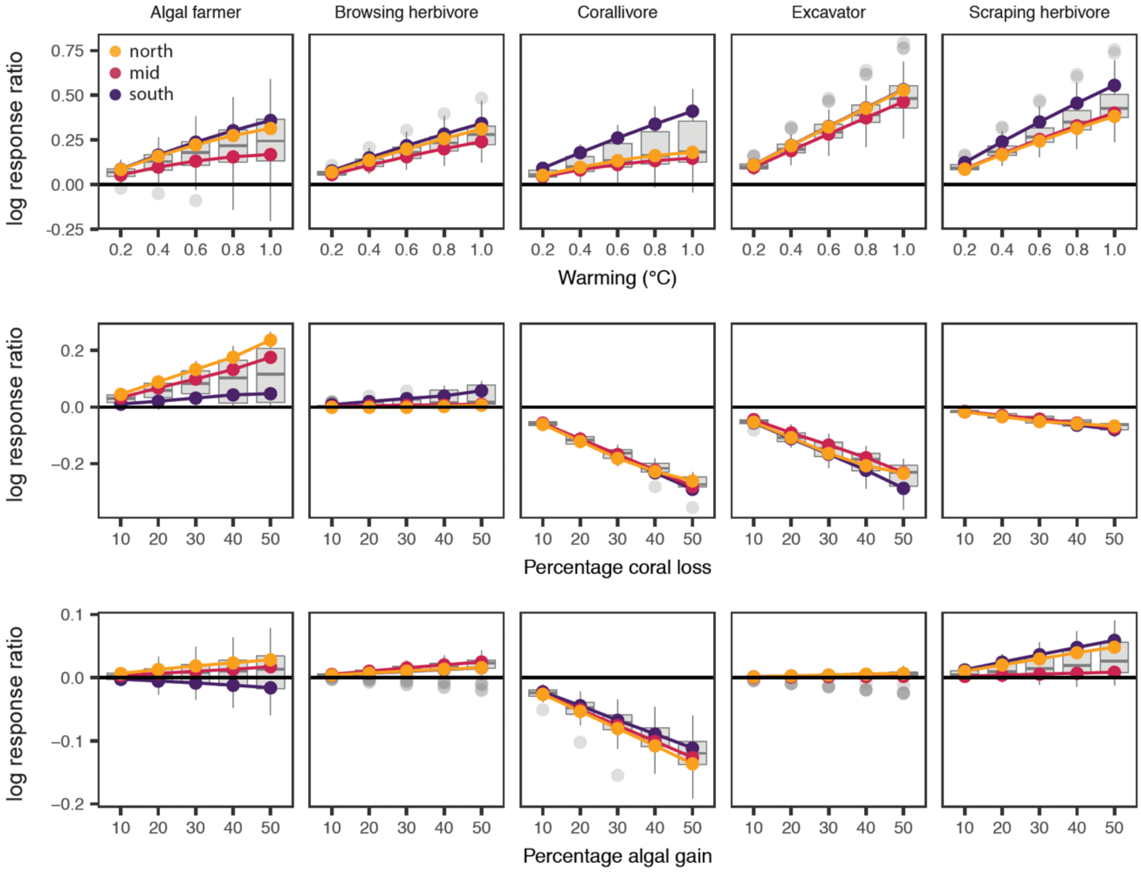

Figure 4.11 Simulated occupancy response of functional groups to standardised environmental change scenarios. Each site on the GBR-CS is exposed to identical environmental changes holding all other covariates constant. Boxplot indicate the distribution of occupancy log-response ratio across all sites. The aggregated response across north, mid, and southern latitudes is indicated by coloured points-and-lines.

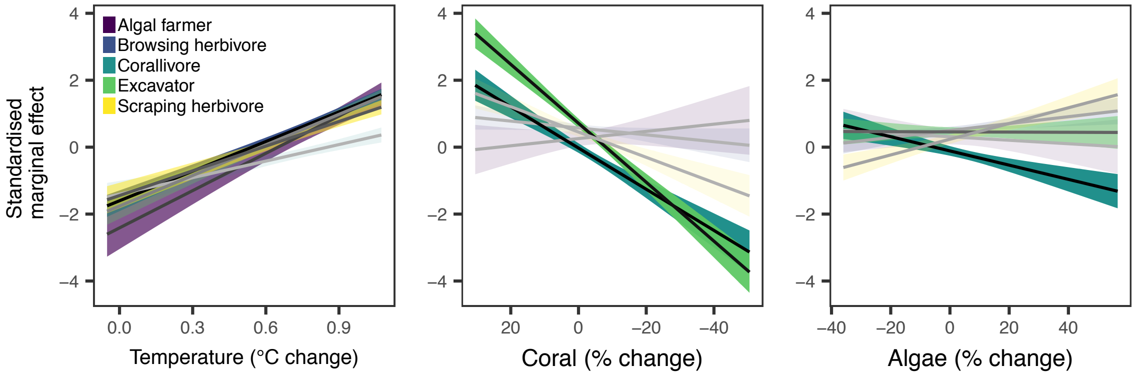

Figure 4.12 Occupancy response of functional groups to environmental changes after the 2015-2016 summer heat event simulated using observed environmental changes. Environmental changes are estimated as the difference between before and after surveys (see Methods, Figure 4.3, 4.4). Standardised marginal effects are the predicted log-occupancy response ratios from multiple regressions. I scale these across all environmental responses to give a comparable effect between different environmental changes and different functional groups. The slope of lines therefore gives the relative effect compared to each other line. Shaded regions are 95% confidence intervals estimated as 1.96 x standard error. Alpha is set to the R^2 value for independent environment by functional group models. Direction of x-axis responses are related to the direction of effect expected with warming. Note that here each site experiences a different combination of environmental changes and I parse the overall effect of these environmental changes on the entire functional group using multiple regressions.

4.5 Discussion

My results indicate how reef fishes' ecosystem functioning may change slowly, showing resistance, in response to heatwave events. First at a species-level, response to multiple environmental changes were variable within each functional group, apart from excavators. Second at a functional-group level, functional groups with a high average species' sensitivity to one stressor, such as live coral cover change, are often positively influenced by warming. Therefore, context-dependent responses to heatwaves may arise that depend on the exact combination of heatwave effects, their relative durations, and initial species composition at a local site (Harborne *et al.*, 2016). Indeed, variable species responses to reef disturbances has been documented in recent meta-analyses (Wilson *et al.*, 2006; Pratchett *et al.*, 2018). Observed responses to heatwaves can be counterintuitive (Wilson *et al.*, 2006; Cheal *et al.*, 2008). For example, corallivores slightly increased in biomass over the 2015-2016 summer heatwave and bleaching event on the GBR-CS (Stuart-Smith *et al.*, 2018). The net effect of temperature alone can be complex to predict, for example, because of differential thermal scaling rates between resources and consumers (Barneche *et al.*, 2014; Gilbert *et al.*, 2014; Bruno *et al.*, 2015): considering biogenic habitat shifts and response diversity too suggests the short-term effects of heatwaves may be difficult to predict *a priori*.

I interpret the spatial homogeneity of response diversity as a form of resilience in corallivores, browsing herbivores and scraping herbivores. If a local assemblage becomes depauperate of a species (and response directions) after a disturbance, others can fill the response 'space' of the ecosystem function through dispersal (even if the underlying species that fulfil this ecosystem function varies, i.e., Cheal *et al.*, 2012, 2013). Warming effects on reefs are spatially heterogeneous (Hughes *et al.*, 2017; Stuart-Smith *et al.*, 2018); homogeneous spatial response diversity leads to pockets of resilient assemblages even if some assemblages are locally extirpated during disturbances. More spatially homogenous response diversity may arise from species' traits that allow higher dispersal distances (larval mode); greater frequency of occurrence (high diet breadth); or, wider thermal niche breadths (wider physiological tolerance) leading to larger geographic ranges (Slayter *et al.*, 2013; Kambach *et al.*, 2019). Homogeneity as a mechanism of regional resilience, by definition, cannot exist on isolated reef systems (Graham *et al.*, 2006; Graham, 2007; Sheppard *et al.*, 2012), suggesting the regional context of response diversity may be important to consider for reef-fish recovery to multiple disturbances. Algae farmers, in contrast to the above groups, had a spatially heterogeneous pattern of response diversity suggesting a greater sensitivity of this ecosystem functional at a regional scale – perhaps due to non-overlapping underlying species distributions (Emslie *et al.*, 2012).

Regional response diversity was filtered into local assemblages for some functional groups (scraping herbivores, browsing herbivores, and corallivores; Table 4.1). Thus, local assembly processes 'realised' the potential resilience of the regional fauna; understanding the mechanisms underpinning this pattern be important for managing locally resilient fauna. A number of non-mutually exclusive factors may contribute. A speciose regional pool that has high response diversity and high local richness (i.e., weak competitive exclusion) may lead to, by chance, a diverse set of responses locally (i.e., in the browsing herbivores, Laliberté *et al.*, 2010). Second, some groups may occur in sites with high habitat heterogeneity that leads to filtering for multiple response directions. Null models examining whether local response diversity is greater than expected by chance may be useful to examine whether environmental filtering acts to determine local response diversity (e.g., Blonder *et al.*, 2015). High dispersal rates would enable regional pools to be well-represented locally, facilitating the above two factors, helping homogenise response diversity between assemblages: the GBR-CS is known to be a well-connected reef system (James *et al.*, 2002).

The lack in response diversity of excavators, at a regional and local scale, identifies the vulnerability of reef bioerosion (Nyström, 2009; Perry *et al.*, 2014). This low response diversity is exacerbated by excavators having a very low number of species providing this ecosystem function, indicating another dimension of resilience is low (i.e., little redundancy in this ecological role, Bellwood *et al.*, 2003). The strong positive association between excavators and coral cover suggests a vulnerability to the predicted declines in coral cover with further heatwave events (De'ath *et al.*, 2012). In contrast, algal-farmers had the highest overall response diversity, and perhaps higher resistance to heatwaves. For example, bleaching in the northern region of the GBR-CS homogenised assemblages towards algal-farmer functional groups (Richardson *et al.*, 2018) and algal-farmers were one of the only groups to increase on the most severely bleached reefs in southern GBR (Cheal *et al.*, 2008). That said, some algae farming territorial damselfish favour high coral cover to establish territories (Pratchett *et al.*, 2011), which may in fact contribute to the response diversity of this group, but sensitivity of particular species.

Most functional groups benefited from warming which goes against the notion that heatwaves degrade reef fish biodiversity (Graham *et al.*, 2006; Pratchett *et al.*, 2018). However, the physiological effects of warmer temperatures can increases organismal performance, up to a threshold (Angilletta *et al.*, 2010; Bruno *et al.*, 2015). Most tropical species have peak abundance in the warmest available temperatures in their geographic range so GBR-CS fishes, on average, benefit from warming (Waldock *et al.*, 2019, Chapter 3). This thermal range context is important in predicting species occupancy and abundance change (Deutsch *et al.*, 2008; Bates *et al.*, 2014a; Stuart-Smith *et al.*, 2015, 2018; Day *et al.*, 2018). Studies often focus on reporting species declines but a substantial proportion of fishes can increase in abundance with warming (i.e., 78% species increase with no change in coral, 50% increase even with loss of coral cover, Emslie *et al.*, 2014; 40% species increase with loss of coral, Wilson *et al.*, 2006a) – these positive effects are generally larger in herbivores as expected based on theory using size-based ecosystem models (Rogers *et al.*, 2018). Obviously, the relative effect of warming may be small, at a local scale, compared with wholesale structural complexity loss and the total loss of corals. During heatwaves, the warming effects may be short-lived. However, if corals recover rapidly, and bleaching rates are low then longer-term climate warming effects may benefit reef fishes on the GBR-CS. My simulations help to disentangle multiple positive and negative aspects of heatwave events for reef fishes, but I strongly caution that structural complexity loss is not considered (Emslie *et al.* 2014), and I do not identify the mechanisms by which temperature may positively influence abundance (but see Bruno *et al.*, 2015).

4.5.1 Limitations

The relevance of response diversity to confer resilience to ecosystem functions depends on whether functional groups provide a coherent and distinct ecosystem function. Instead, unique functional trait combinations suggest that species may each contribute to mostly unique ecological roles, inferred to represent ecosystem functions (Mouillot *et al.*, 2014). As such, the resilience of an ecosystem function may be sensitive to that one species' environmental response (i.e., response diversity = 0). Species richness can increase ecosystem functions (i.e., herbivory rates) which suggests that species do have, to some extent, unique contributions (Lefcheck *et al.*, 2019). However, that functional traits may strongly represent ecosystem functions is often criticised (Mlambo, 2014) and resource partitioning may only occur when co-occurring species' interact and are at high abundance (Griffin *et al.*, 2008). The linkage between response diversity and the extent of species' partitioning of ecosystem functions remains poorly established, but is essential to develop to test the relevance of response diversity concepts (Díaz *et al.*, 2013 i.e., how often does response diversity = 0 because of strong resource partitioning).

I assume species' response to spatial environmental gradients represents their response to temporal environmental changes, i.e., a space-for-time assumption (Damgaard, 2019).

Space-for-time ignores how temporal environmental dynamics and assume species' environments are constant or stationary, and therefore that communities are at equilibrium with their environment. The high-disturbance regimes of coral reefs suggest that this assumption is unlikely to be valid. Here, disturbances would decrease the ability to detect signals from the noise, rather than systematically bias response diversity, and so are unlikely to systematically bias our results. Because of this statistical noise response diversity may be underestimated here, relative to the true effect of spatial environmental variation on species occurrences (if fewer significant spatial relationships are observed). Space-for-time has strengths compared to a before-after approach in our instance, particularly compared to studies using short time-periods after environmental change. First, lags in population declines due to sub-lethal effects of heatwaves may underestimate abundance change using before-after approaches (Wilson *et al.*, 2006b). Second, subtle longer-term effects that improve body condition may not be well-captured in before-after surveys (Rogers *et al.*, 2018). Finally, before-after may underestimate the potential for population increases because recruitment to newly suitable environmental conditions is lagged (Aalto *et al.*, 2015; but see Graham *et al.*, 2007). Species establishment in new portions of geographic ranges requires that new settlement environments develop and that sporadic chance events occur - these are events poorly captured by short-term before-after designs (Bates *et al.*, 2014c,b; Feary *et al.*, 2014).

4.5.2 Outlook

I offer a framework for assessing response diversity in ecological assemblages by quantifying the effect of spatial environment gradients on whole assemblages (implemented in HMSC, Ovaskainen *et al.*, 2017). An advantage of this approach is that I do not assume 'functional response traits' represent species responses to environmental change – an assumption that is often not directly demonstrated (e.g., Laliberté *et al.*, 2010a; Richardson *et al.*, 2018; but see Kühsel & Blüthgen, 2015). Instead, I used realised niches as a representation of species responses to environmental change which inherently validates the assumption that traits measure environmental responses (Kühsel & Blüthgen, 2015). Therefore, species' realised niche diversity, based on species environmental distributions, may be an easily quantified and conceptually accurate measure of community response diversity (Kühsel & Blüthgen, 2015; Dee *et al.*, 2016). Future work should upscale the variability in species' niches and community response diversity, investigated here, to the provisioning of ecosystem functions and services in the face of global change (Dee *et al.*, 2016). Such insights are needed to maintain ecosystem functions during the increased intensity, frequency and extent of heatwaves during the ongoing Anthropogenic climate crisis (Hoegh-Guldberg *et al.*, 2018; Smale *et al.*, 2019).

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Chapter 5 Refining the ‘wide-ranged winners’ paradigm: Multiple aspects of insect realised niches predict species’ sensitivity to land-use change

5.1 Abstract

Why geographic range size predicts species’ response to land-use change and intensification is not yet established. Many correlates of larger geographic ranges, such as environmental niche breadth, may mediate species response to environmental change. Agricultural land uses have warm and dry microclimates, compared to cooler and wetter primary forests, so are predicted to filter for species with broader niches that are tolerant of warmer and drier environments. For 712 insect species I model occurrences between forest and agricultural land-uses in 275 local assemblages. I test whether the effect of land-use on occurrence rates depends on the properties of species geographic range or realised niches. Species’ occurrence amongst land-use types was predicted better by species’ environmental niche properties than geographic range size. The predicted species’ niche effects consistently matched the expected direction of microclimatic transition from forest to agriculture. For example, species with niche limits in warmer climates had higher occurrence rates in agricultural land-use. Despite clear overall niche effects, the most important dimension of a species’ realised niche was highly context-dependent. This heterogeneity likely reflects the variety of taxonomic groups and regions used in this analysis. Thus, niches may help explain the syndrome of ‘wide-ranged winners’ under environmental change. However, multiple components of the species environmental niche may be important to consider. Environmental niche properties derived from species’ geographic distributions can be a simple, widely applicable, and predictive tool to help identify when biodiversity responds to the microclimate component of land-use change.

5.2 Introduction

Trait-based assembly rules have a long history in ecology (MacArthur, 1958; Tilman, 1977; Leibold *et al.*, 2004). Trait-based mechanisms underpin responses to environmental changes if trait-environment interactions affect demographic rates that in turn influence population dynamics, local species' occupancy rates and community composition (Webb *et al.*, 2010; Salguero-Gómez *et al.*, 2018). The lens of species' traits may allow clearer predictions of how environmental change will affect biodiversity.

Species traits are often important in determining which species are tolerant of or sensitive to land-use change (Meynard *et al.*, 2011; De Palma *et al.*, 2015). An often-supported prediction is that local communities in agricultural land uses are comprised of environmental generalists, with wider geographic ranges (Cleary & Mooers, 2006; Scott *et al.*, 2006; Cofre *et al.*, 2007; Nowakowski *et al.*, 2017; Newbold *et al.*, 2018). Land-use change that removes forest cover causes a shift to microclimates that are on average warmer, drier, and more diurnally and seasonally variable in temperature (Chen *et al.*, 1999; Hardwick *et al.*, 2015; Latimer & Zuckerberg, 2017; Senior *et al.*, 2017; De Frenne *et al.*, 2019). These microclimatic shift can cause 5-10°C difference in maximum temperatures between land-use types (Senior *et al.*, 2017; De Frenne *et al.*, 2019). This microclimatic shift sets up several predictions for how trait-environment interactions influence local communities (Woods *et al.*, 2015; Pincebourde *et al.*, 2016). For example, we expect an increase in the occurrence and abundance of species with tolerance of warm and dry environments, with land-use transition from primary forest to agriculture. Species whose performance optima and critical limits are at higher temperatures persist more frequently in agricultural landscapes (Frishkoff *et al.*, 2015; Nowakowski *et al.*, 2017, 2018), leading to assemblages containing, on average, more species with ranges centred in warmer regions (Barnagaud *et al.*, 2013).

Geographic range size is expected to predict species' response to land-use change because of the trait complexes that drive larger ranges. However, large geographic range can act as a catch-all for multiple trait syndromes which means that untangling the trait-based mechanisms shared by geographic range size and land-use sensitivity is challenging (Bartomeus *et al.*, 2013; Laube *et al.*, 2013; Newbold *et al.*, 2013, 2015; Rader *et al.*, 2014). Furthermore, traits such as morphology and behaviour are difficult to compare between different taxonomic groups (Verberk *et al.*, 2013; Wong *et al.*, 2018)

The same responses to land-use change (i.e., a positive effect) can arise through different trait complexes (Díaz *et al.*, 2013). Species with wider geographic ranges often have wider niche breadths (Slayter *et al.*, 2013; Kambach *et al.*, 2019) and range limits are expected to be driven by environmental tolerance limits (Lee-Yaw *et al.*, 2016). Niche limits inferred from species distributions may therefore better predict species response to land-use change than species' geographic range size, but this hypothesis remains untested. If one's aim is to generalise trait-by-land use responses, then species' environmental niche limits provide excellent candidate traits.

Here I test whether species realised niche limits, defined from the environmental parameters of species' distributions, predict species occupancy rates in forest (cool-wet-stable) and agricultural (warm-dry-variable) environments, which are characteristic of land-use change. I test for this pattern in over 700 insect species worldwide. Insects are an excellent model for a number of reasons. First, ectothermic thermoregulation means that occurrence is likely to depend strongly on temperature. Second, the diversity of insects makes finding comparable traits amongst taxonomic groups challenging. Thus, a key aim of this paper is to test if simple and fully general species properties, such as realised environmental niche traits, can predict occurrence across gradients of land-use. Third, there is an urgent need to identify the potential mechanisms underpinning recent insect biomass declines (Hallmann *et al.*, 2017; Lister & Garcia, 2018).

Establishing how species traits (here, geographic range size and realised niche limits) interact with the local environment to determine community dynamics remains a major challenge (Jamil *et al.*, 2013; Peres-Neto *et al.*, 2017). Statistical challenges arise because environmental gradients are measured at the site level but traits are measured at the species level (Miller *et al.*, 2019). One of the most common approaches is to estimate weighted mean trait values for the whole community at a site and regress this value against environmental gradients (i.e., Funk *et al.*, 2017). However, community-weighted mean trait values can strongly inflate the likelihood of type-1 error because the pseudo-replication of species amongst sites is not accounted for (Miller *et al.*, 2019). Here, I instead use a multi-level model based approach to provide a more robust assessment of trait-environment interactions and retains a focus on species-level traits (Jamil *et al.*, 2013; Miller *et al.*, 2019).

My first aim is to test if species' occupancy between primary and mature forest and agricultural sites depends on properties of species' geographic ranges and realised niche. We then quantify, for the first time, whether species' occupancy between land-use types is better predicted by their environmental niche traits or their geographic range size. This is predicted if the environmental (i.e., temperature and moisture) differences between land-use types is an important driver of local species occurrence patterns. Finally, I also compare these effects across breadth (e.g., range size) and location (e.g., range centre) metrics of species' geographic range and realised niches. In general, I aim to establish whether realised niches estimated from coarse distribution data are a useful tool in predicting biodiversity change, this is important in under-sampled groups such as insects (Ballesteros-Mejia *et al.*, 2013) and could identify how relatively low-cost sources of distribution data (i.e., citizen science projects) can be used more widely (Amano *et al.*, 2016). I find that realised niches are generally predictive of occupancy across land-use gradients but that niche effects were often context-dependent: predicting which particular aspects of species' realised niche cause sensitivity to land-use change, and why, remains a major challenge for future research.

5.3 Methods and materials

5.3.1 Species occurrences in land-use types

I extracted insect occurrences from the Projecting Responses of Ecological Diversity in Changing Terrestrial Systems (PREDICTS) database, accessed in July 2017 (Hudson *et al.*, 2014, 2017). PREDICTS provided space-for-time comparisons of assemblage diversity in response to land-use change. I filtered the PREDICTS dataset to include only insect species where binomial names are recorded in full to match with sources of species distribution data (see Global Biodiversity Information Facility, GBIF, data description below). I included only estimates of species' abundance, density or occurrence at a site where multiple species were recorded to ensure studies are focussed on communities. I converted abundances to presence-absences. Further, I removed species with no available distribution data and filtered out sites that have less than 40% of species and individuals with distribution data available. This step ensured a high coverage of species in an assemblage with geographic range and realised niche information. I included only the land-use classes of primary forest, mature secondary forest, plantation forest, pasture and cropland (for further details see appendicies in Hudson *et al.*, 2014) to ensure: i) models were not overly-complicated by land-use classes with few data in the PREDICTS database (i.e., Urban), ii) we retained land uses for which the direction of thermal change was most distinct. Primary forest is native forest not known to have ever been completely destroyed by human activities, mature secondary forest has recovered to similar structural complexity of primary forest but is known to have been fully removed but has recovered. Plantation forests refer land used for crop trees and shrubs, cropland are predominantly herbaceous crops, and pasture is land used for livestock grazing. I ensured each study had one primary forest site for comparison and at least two sites in total. I combined mature secondary forest and primary forest, which have been shown to contain equivalent levels of richness and abundance (Newbold *et al.*, 2015), into a 'mature forest' land-use type. I combined plantation forest, pasture and cropland into a 'agriculture' land-use type (note that 0.1% observations were from eucalyptus plantations). I ensured sites were within forested biomes (based on The Nature Conservancy 2009 definitions) to compare the relative occurrences in mature forest to agriculture (rather than primary vegetation in general i.e., open habitats). This step ensured I study land-use transitions where the greatest change in environmental conditions is expected to occur, from forests to agriculture (Senior *et al.* 2017). In total, I analysed 19 studies containing 275 sites and 712 species. The mean number of sites per study was 14 (2-110). This gave a total of 18,595 site by species observations. Most observations were from Lepidoptera and Coleoptera taxonomic groups, and the Palearctic and Nearctic were the most commonly studied realms (Appendix 4 Figure S1). Note, three studies provide 85% observations, therefore I perform sensitivity tests to examine the influence of data-rich studies (see below; Baur *et al*. 2006; Meijer *et al.* 2011; Cabra *et al.* 2012).

5.3.2 Estimating metrics of geographic range and realised niche

Geographic distributions of the species in the PREDICTS database extract were estimated from occurrence records held in GBIF (www.gbif.org), accessed on the 25th July 2017 (provided by Dr. Tim Newbold). I excluded all species with fewer than 20 GBIF records that were unique to 0.1° x 0.1° grid cells, giving a median of 304 occurrence records per species (5th percentile = 29; 95th percentile = 5221; Appendix 4 Figure S2). The median number of species occurrences records per study was 464, suggesting that most species in a given study have a high number of occurrence records and a relatively well sampled geographic range and realised niche (Wisz *et al.*, 2008; Feeley & Silman, 2011). The low cut-off of 20 presence records was also appropriate given my aim of testing simple measures of species distributions from a taxonomic group with relatively sparse sampling and high levels of inventory incompleteness (Ballesteros-Mejia *et al.*, 2013). I intentionally did not fit species distribution models (SDMs) because I aim only to define the edges of realised niches. To obtain environmental distributions of the 712 species that remained in the dataset, I matched their GBIF occurrence records with rasterised environmental variables in WorldClim v2.0 at a 1 km scale at the equator (~0.01°; Fick & Hijmans 2017). For temperature measures I extracted annual mean, monthly minimum and monthly maximum temperatures. For precipitation measures I extracted annual total precipitation and total precipitation in the wettest and driest months, for all 1km grid cells in which a species was observed.

I characterised 28 metrics of species geographic ranges and realised niches (based on species geographic and environmental distributions). These are defined fully in Table 5.1 and Figure 5.1. This set includes conceptually distinct metrics (Gaston and Fuller 2009). For example, EOO is defined as “overall geographic spread of the localities at which a species occurs” and provided a simple measure of a species ability to occupy broad areas. AOO is the area of occupied habitat which is, by definition, never larger than EOO. Both have different assumptions; for example, the value of AOO is strongly influenced by the size of grid cells used, whereas EOO ignores range discontinuities and thereby includes areas species may never occupy (Gaston & Fuller, 2009). The hypothesised effects of each metrics are presented in Table 5.1. Broadly, all geographic range and realised niche breadth measures were expected to increase occupancy in sites with agricultural land uses. Species having warmer and drier average realised niches and realised niches with higher maximum temperatures and lower minimum rainfall were expected to have positive effects on occupancy in agricultural land uses. Species having lower minimum temperatures were expected to have higher occupancy in agricultural land uses because of decreased minimum local temperatures. Species with realised niches having high precipitation in wet and dry seasons should have higher occupancy in mature forests.

From the set of 28 metrics, I grouped by geographic range or realised niche ‘location’ or ‘breadth’ (Table 5.1). These are conceptually different measures of species realised niches and geographic ranges. ‘Location’ metrics measured the central tendency or extremes of species geographic ranges or realised niches. ‘Breadth’ metrics quantified variation in species geographic range or realised niches. For example, T_{opt} was a

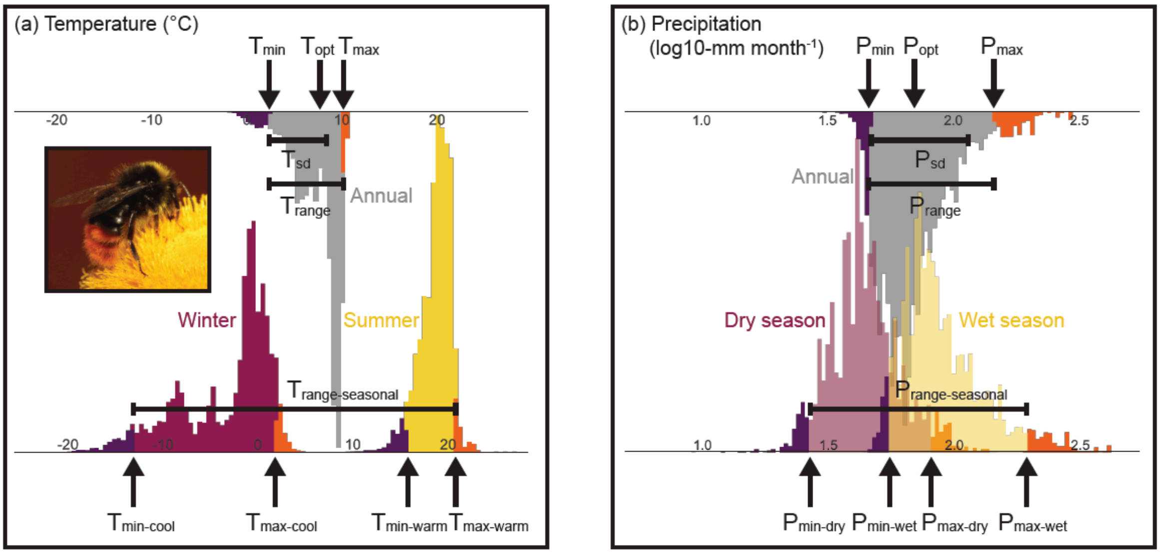

Figure 5.1 Realised niche metrics illustrated for *Bombus pratorum.* Occurrences were obtained from GBIF and matched with environmental rasters to show annual and seasonal variation limits for (a) temperature and (b) precipitation. Acronyms are described in Table 5.1. Photo credit: Donald Hobern from Copenhagen, Denmark via Wikimedia Commons.

Table 5.1 28 metrics of geographic range and realised niches with hypothesised direction of effects in agricultural land uses.

	Group	Metric	Method	Direction in agricultural land use
Geographic	Breadth	AOO_{11}	Sum of occupied 11km x 11km grid cells*	+
	Breadth	AOO_{110}	Sum of occupied 110km x 110km grid cells*	+
	Breadth	EOO_{11}	Sum of 11km x 11km grid cells between continentally constrained latitudinal limits*	+
	Breadth	EOO_{110}	Sum of 110km x 110km grid cells between continentally constrained latitudinal limits*	+
	Breadth	L_{sd}	Standard deviation of latitudes of occurrences	+
	Location	L_{opt}	Mean latitude of occurrences	+
	Location	L_{min}	5th quantile absolute latitude of occurrences	-
	Location	L_{max}	95th quantile absolute latitude of occurrences	+
Thermal	Location	T_{opt}	Mean annual temperature	+
	Location	T_{min}	5th quantile of annual temperature	-
	Location	T_{max}	95th quantile of annual temperature	+
	Location	$T_{min\text{-}cool}$	5th quantile of minimum monthly temperature	-
	Location	$T_{max\text{-}cool}$	95th quantile of minimum monthly temperature	+
	Location	$T_{min\text{-}warm}$	5th quantile of maximum monthly temperature	-
	Location	$T_{max\text{-}warm}$	95th quantile of maximum monthly temperature	+
	Breadth	T_{sd}	Standard deviation of annual temperature	+
	Breadth	T_{range}	T_{max} - T_{min}	+
	Breadth	$T_{range\text{-}seasonal}$	$T_{max\text{-}wet}$ - $T_{min\text{-}dry}$	+
Precipitation	Location	P_{opt}	Mean annual precipitation	-
	Location	P_{min}	5th quantile of annual precipitation	+
	Location	P_{max}	95th quantile of annual precipitation	-
	Location	$P_{min\text{-}dry}$	5th quantile of minimum monthly precipitation	+
	Location	$P_{max\text{-}dry}$	95th quantile of minimum monthly precipitation	-
	Location	$P_{min\text{-}wet}$	5th quantile of maximum monthly precipitation	+
	Location	$P_{max\text{-}wet}$	95th quantile of maximum monthly precipitation	-
	Breadth	P_{sd}	Standard deviation of annual precipitation	+
	Breadth	P_{range}	P_{max} - P_{min}	+
	Breadth	$P_{range\text{-}seasonal}$	$P_{max\text{-}wet}$ - $P_{min\text{-}dry}$	+

*see Newbold et al 2018 for full details on estimating these metrics.

measure of thermal realised niche location, whereas T_{sd} was a measure of thermal realised niche breadth.

To compare the effect of variation in geographic range and realised niche metrics within a study, realised niche and geographic range metrics per species were standardised within each study. For each metric I subtracted the study-level mean and divided by the within-study standard deviation. This step also helped reduce model multicollinearity by considering only variation between metrics within the study species pool, thus removing some of the correlation that occurs across broad geographic gradients when the species pool is considered globally (Appendix 4 Figure S3).

5.3.3 Statistical models

I first analysed the full dataset following the workflow described below (5.3.3.1). Next, because of the relatively low number of studies compared to other analyses with the PREDICTS datasets, I performed sensitivity tests to examine if particular studies strongly influenced the main results. I refitted models with influential studies excluded (5.3.3.2). Finally, to examine whether geographic ranges and realised niches exhibited context-dependent effects I used a set of 6 case studies that had a relatively high number of sites and species from our pool of studies. Figure 5.2 shows the workflow of this manuscript.

I fitted binomial generalised linear mixed-effects models (GLMMs) to test how species' occupancy depends on the interaction between land-use type and species geographic range or realised niche. I used the GLMM approach of Jamil *et al.* (2013) to understand how ecological responses to environmental variation depends on species geographic range or realised niche metrics. GLMMs produce better type-1 error control and higher statistical power when compared to community-weighted mean correlations or matrix-correlation (i.e., fourth-corner) approaches with similar aims (Miller and Ives 2018).

I modelled species' presence as a function of land use interacting with species geographic range and realised niche metrics. The full GLMM structure was:

$$(1) \qquad \mathrm{logit}(p_{ij}) = a_0 + (a_1 z_j) + (b_0 + \varepsilon_{\beta_j})x_{hi} + (b_1 z_j x_{hi}) + \varepsilon_{\alpha j} + \gamma_{hi}$$

which described the (logit-transformed) probability of occurrence (p) in site *i*, for species j, as a linear function of geographic range or realised niche metric (z), the land-use type (x) and the interaction between land use and range metric (xz – a trait-environment interaction). I included random intercepts for species ($\varepsilon_{\alpha j}$) crossed with a random intercept of sites nested in blocks (γ_{hi}) in addition, to a random slope which described variation among species' responses to land-use type ($\varepsilon_{\beta_j} x_{hi}$). I fitted a study random effect which accounted for important sources of environmental and methodological differences amongst studies. Our results were unlikely to be influenced by using study-level rather than block-level random effects because refitting initial models at a block level had a small influence on fixed-effect values (e.g., average change of order 10^{-4}) and only 4 studies have > 1 block. The complexity of a species-specific random slope was supported by likelihood-ratio tests using restricted estimates of maximum likelihood (REML). Jamil *et al.* (2013) discuss modelling details.

5.3.3.1 Testing trait-environment interactions

I aimed to reduce the full set of 28 metrics considered. I first ran 28 models, one model for each of the 28 geographic range and realised niche metrics, and tested whether each trait-environment interaction terms (i.e., land use *x* range/niche metric) explained a significant proportion of variation in species occurrences (Appendix 4 Table S1). The significance of each trait-environment interaction was determined by fitting models using maximum likelihood and performing likelihood-ratio tests using the X^2 statistic to obtain p-values at an alpha of 0.05. I also assessed model AIC and marginal R^2 values (Nakagawa & Schielzeth, 2013).

Next, for temperature, precipitation, and geographic distributions within a location and breadth category, I identified the metric with greatest explanatory power based on the X^2 statistic, giving a total of 6 metrics. This covariate refinement was performed to identify a candidate set of trait-environment interactions likely to be important for species' occupancy across land-use types; and to test whether geographic range or realised niche metrics better predict occurrence across land-use gradients. For example, the 6 metrics selected in the full dataset were $T_{max\text{-}warm}$, $T_{range\text{-}s}$, P_{min}, $P_{range\text{-}s}$, L_{opt}, and L_{sd} (see Appendix 4 Table S1).

I fitted models with the 6 trait-environment interaction terms identified above. Models were fit using maximum likelihood and I performed likelihood-ratio tests by dropping each term from this model in turn to estimate X^2 and change in AIC values. Because I aimed simply to test whether geographic range or realised niche metrics better predict occupancy across land-use types, rather than finding a minimum adequate model, I did not perform further refinement of covariates (i.e., model selection). Not performing model selection is justified in this case as each metric has clear hypothesised effect, and our goal is not prediction, for which identifying a minimum adequate model is necessary (Whittingham *et al.*, 2006). In addition, model selection can lead to greater certainty in model coefficients than warranted, even with relatively weak collinearity (Morrissey & Ruxton, 2018). Strong multicollinearity was not indicated: all pairwise correlations between focal geographic range and realised niche metrics were < 0.7 and all variance inflation factors (VIFs) < 3 (Imdadullah *et al.* 2016).

5.3.3.2 Sensitivity analysis

The PREDICTS database contains data from a very heterogeneous set of insects, sampled in very heterogeneous ways in very different environmental settings. I therefore tested my initial findings were sensitive to these different contexts. I performed an influence analysis by refitting my model but jack-knifing at the study level. I performed sensitivity analyses by estimated the Cook's distance. I refitted the modelling process (i.e., step 5.3.3.1) but removed any studies that had a Cook's distance > 1 for the trait-environment interaction parameters (Cook's distance is a measure of overall influence of a study on all parameters of interest, see Appendix 4 Figure S4). In this reduced data subset, I analysed 18 studies containing 267 sites and 434 species, giving a total of 16,235 site by species observations.

5.3.3.3 Case studies

Fitting the above global models allowed the estimation of overall effects of geographic range and realised niche metrics, missing any heterogeneity of effects among studies. The small number of studies in the final data, through pruning the full PREDICTS dataset, may have exacerbated this issue. Therefore, the presence of an effect of geographic range and realised niches may be poorly estimated in a global-model framework unless there is strong agreement in the direction of trait-environment interactions amongst studies. Strong agreement may be unlikely given the heterogeneous comparisons across regions, insect taxa and sampling methodologies in PREDICTS and therefore context-dependencies may be more likely. Several studies were well-replicated enough, having more than 30 species in addition to more than 100 observations, to be amenable to independent analyses; in these I examined potential context-dependent effects. I

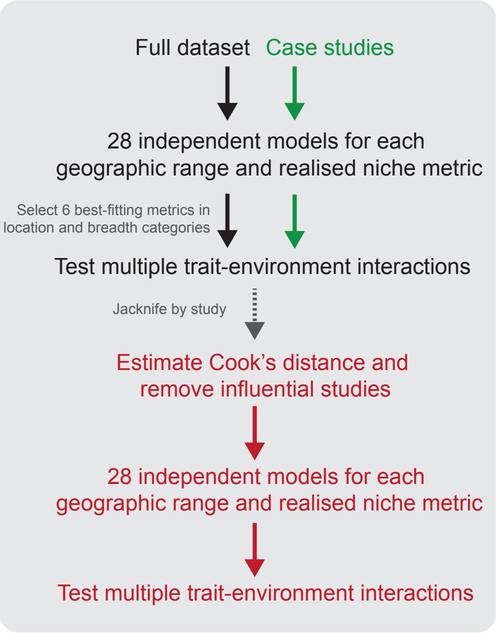

Figure 5.2 Schematic of the analysis workflow. For the full dataset, and the case-study data subsets, I used the same workflow detailed in the methods. From the final model with the full dataset I performed a sensitivity analysis (red) therefore, two sets of results are provided in the main manuscript, and a set of results for the case-studies.

analysed these studies as independent case-studies and tested if trait-environment interactions differed amongst studies. The five studies I used were Baur *et al.*, (2006), Barlow *et al.*, (2007), Vu (2009), Meijer *et al.*, (2011), Cabra-García *et al.*, (2012). I separated Baur *et al.* 2006 into two separate case studies for day-flying and night-flying Lepidoptera, giving an total of 6 case-studies. I followed the same modelling procedure as above (Figure 5.2), but only retained significant trait-environment terms in the final models because we are using fewer data. Pairwise correlations between geographic range and realised niche metrics within case-studies were sometimes > 0.7, or VIFs were > 3 and if so I removed the least explanatory variables indicated by X^2 values in independent models. Further, in Baur *et al.* (2006) I included both $T_{min\text{-}warm}$ and $T_{max\text{-}warm}$ for thermal realised niche location metrics because both models X^2 values were almost identical, but the hypothesised effects were opposite in direction and strong collinearity was not indicated. I used block-level random effects where studies had multiple blocks.

All analysis were performed in R (version 3.4.0), I used the package 'glmmTMB' to fit statistical models (Brooks *et al.*, 2017) and 'lme4' to fit models during the jacknifed sensitivity analyses to estimate Cook's distance (Bates *et al.*, 2015).

5.4 Results

Our first analysis identified that only $T_{max\text{-}warm}$ significantly affected species' occupancy through a trait-environment interaction across land-use types (Figure 5.3, Table 5.2, see Appendix 4 Table S1 for independent model fits). Occupancy in agricultural land use relative to mature forest was significantly higher for species with relatively warm summer limits compared to other species in the community. In this global model, species' thermal realised niches were much more important than their precipitation realised niche or geographic range metrics in shaping how land-use change affects occupancy (Table 5.2).

However, the sensitivity analysis revealed that this initial result was dependent on the inclusion of a single study (Baur *et al.*, 2006) which strongly influenced the model parameters (Appendix 4 Figure S4). When modelling was repeated with this study excluded, only $P_{min\text{-}wet}$ significantly affected species occupancy through a trait-environment interaction across land-use types (Figure 5.4, Table 5.2). Dry-affinity species were favoured in agricultural land use. Interestingly, fitting geographic range effects independently identified a significant positive relationship between AOO_{110} and occurrence in agricultural land use (Appendix 4 Table S2). However, this effect was no longer important in models that also included $P_{min\text{-}wet}$, which suggests that the initial relation between AOO_{110} and occurrence was an artefact of the unmeasured niche effects, in this case.

Further investigating such context dependencies, through examining effects within studies independently, revealed that 4 out of 6 case studies supported significant trait-environment interactions. However, the particular trait-environment interaction that was most important varied amongst studies. Niche trait-environment interactions were more frequently supported than geographic range trait-environment interactions. Furthermore, niche trait-environment interactions were frequently in the expected directions that match microclimatic changes across land-use gradients: agricultural practises benefit species with warmer-warm limits, cooler-cool limits, drier affinities and broader environmental preferences (Table 5.3). All effects found by regression with multiple trait-environment interactions were qualitatively consistent with these hypotheses (Figure 5.4; Table 5.1), perhaps suggesting that the exceptions in the single trait-environment interaction regressions may have reflected correlations among geographic range and realised niche metrics. Geographic range size was generally identified less frequently than realised niche effects, but was important in one study of day-flying Lepidoptera (Baur *et al.*, 2006).

Table 5.2. Results of likelihood-ratio tests for the main model with trait-environment interaction terms for 6 geographic range and realised niche metrics. Metric column represents the trait used in a land-use by trait interactions (i.e., trait-environment interaction). X^2 and p-values are derived from likelihood ratio-tests with 1 degree of freedom. ΔAIC values is the difference in AIC between models including the focal trait-environment interaction term minus the AIC of models excluding the term.

	First round models			***Sensitivity test***		
Metric	**X^2 (1 d.f.)**	**ΔAIC**	***p***	**X^2 (1 d.f.)**	**ΔAIC**	***p***
$T_{max\text{-}warm}$	**9.9**	**-7.9**	**<0.01**	1.9	0.1	>0.05
$T_{range\text{-}s}$	2.6	-0.6	>0.05	0.2	1.8	>0.05
P_{min}	0.3	1.7	>0.05			
$P_{min\text{-}wet}$				**6.9**	**-4.9**	**<0.01**
$P_{range\text{-}s}$	3.6	-1.6	>0.05	3.7	-1.7	>0.05
L_{opt}	1.6	0.4	>0.05			
L_{max}				0.2	1.8	>0.05
L_{sd}	0.7	1.3	>0.05			
AOO_{110km}				0.9	1.0	>0.05

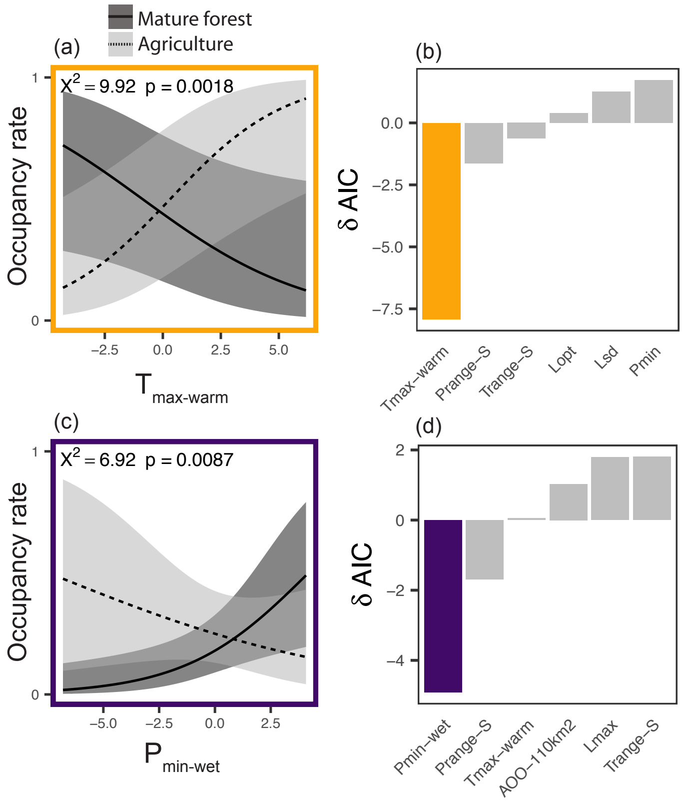

Figure 5.3 Fitted relationship for trait-environment interactions in first round of models (a-b) and after excluding influential studies identified through sensitivity tests (c-d). (a) occupancy rates in different land-use types initially depends on species' $T_{max\text{-}warm}$ which has the greatest reduction in AIC values (b). After excluding influential studies identified in sensitivity tests, $P_{min\text{-}wet}$ is the most important realised niche metric (c-d). X^2 statistics with 1-degree of freedom. *p*-values indicate significance of trait-environment interaction terms. Effects shown are marginal effects when all 6 geographic range and niche metrics are held at their mean values. Shaded regions are 95% confidence intervals.

Table 5.3 Summary of independent models for each geographic range and realised niche trait-environment interaction fitted to each case study. Summaries of case studies are presented in the table header. Blue values are consistent with the direction of effect hypothesised, orange are inconsistent. Blank cells are given where a model did not converge.

		Baur et al. 2006			Meijer et al. 2011			Baur et al. 2006			Vu et al. 2009			Cabra et al. 2012			Barlow et al. 2007		
Order		Lepidoptera (night)			Multiple			Lepidoptera (day)			Lepidoptera			Hymenoptera (Formicidae)			Lepidoptera		
Region		Romania			Azores			Romania			Vietnam			Colombia			Brazil		
N-observations		2360			12100			480			156			1334			546		
N-sites		8			110			8			3			29			13		
N-species		294			110			60			52			46			42		
Locations per species		2847			875			8120			479			231			162		
		Coef.	**s.e.**	***p***	**Coef.**	**s.e.**	***p***	**Coef.**	**s.e.**	***p***	**Coef.**	**s.e.**	***p***	**Coef.**	**s.e.**	***p***	**Coef.**	**s.e.**	***p***
T-location	**Topt**	-0.04	0.44	0.94	0.38	0.27	0.15	-0.01	0.50	0.98	0.11	0.39		0.11	0.39	0.78	-0.06	0.41	
	Tmin	-0.47	0.44	0.28	0.32	0.27	0.25	-0.20	0.48	0.68	-0.01	0.40		-0.44	0.36	0.22	0.07	0.42	
	Tmax	-0.11	0.45	0.81	-0.06	0.28	0.82	0.68	0.51	0.18	0.12	0.38		**1.19**	**0.33**	**0.00**	0.00	0.47	
	Tmin-warm	**-1.45**	**0.44**	**0.00**	0.45	0.26	0.09	-0.01	0.49	0.98	0.14	0.40		-0.20	0.36	0.59	0.05	0.37	
	Tmax-warm	**1.43**	**0.43**	**0.00**	0.04	0.27	0.88	0.54	0.54	0.31	0.17	0.40		**0.99**	**0.37**	**0.01**	0.53	0.44	
	Tmin-cool	0.24	0.44	0.58	0.31	0.28	0.27	-0.20	0.48	0.68	-0.03	0.40		**-0.78**	**0.34**	**0.02**	-0.15	0.42	
	Tmax-cool	-0.43	0.45	0.33	-0.17	0.28	0.54	0.69	0.53	0.19	0.12	0.38	0.74	0.64	0.36	0.08	-0.02	0.48	
T-breadth	**Tsd**	0.30	0.44	0.50	-0.28	0.28	0.33	0.75	0.49	0.12	-0.14	0.43		**0.70**	**0.35**	**0.05**	0.12	0.44	0.79
	Trange	0.40	0.44	0.36	-0.28	0.28	0.33	0.58	0.49	0.24	0.15	0.42		**0.69**	**0.34**	**0.05**	-0.06	0.43	0.90
	Trange-s	0.62	0.44	0.16	-0.17	0.28	0.55	0.44	0.48	0.36	0.11	0.41	0.79	**0.93**	**0.34**	**0.01**	0.33	0.42	0.47
P-location	**Popt**	**0.97**	**0.44**	**0.03**	**-0.87**	**0.26**	**0.00**	-0.14	0.48	0.78	-0.39	0.40		-0.63	0.36	0.08	-0.09	0.40	
	Pmin	-0.27	0.44	0.53	-0.11	0.27	0.70	-0.96	0.51	0.05	-0.81	0.47		**-1.22**	**0.42**	**0.00**	-0.24	0.42	
	Pmax	0.42	0.44	0.34	**-1.03**	**0.27**	**0.00**	0.79	0.51	0.12	-0.23	0.39	0.55	-0.15	0.35	0.66	0.05	0.40	0.91
	Pmin-dry	-0.39	0.42	0.35	0.08	0.27	0.77	-0.67	0.60	0.25	-0.59	0.46		**-0.91**	**0.35**	**0.01**	0.17	0.43	
	Pmax-dry	0.05	0.44	0.91	**-1.06**	**0.27**	**0.00**	0.87	0.50	0.08	-0.29	0.41		0.14	0.34	0.68	-0.06	0.42	0.88
	Pmin-wet	0.44	0.44	0.32	-0.42	0.28	0.13	-0.84	0.48	0.07	-0.56	0.44		**-1.05**	**0.38**	**0.00**	-0.24	0.41	
	Pmax-wet	0.30	0.45	0.50	**-0.79**	**0.28**	**0.00**	0.78	0.51	0.12	-0.09	0.41		-0.31	0.36	0.40	0.45	0.42	0.27
P-breadth	**Psd**	-0.01	0.44	0.97	**-0.90**	**0.28**	**0.00**	**1.05**	**0.51**	**0.03**	0.11	0.40		0.38	0.34	0.27	0.28	0.40	
	Prange	0.54	0.44	0.22	**-0.98**	**0.28**	**0.00**	**1.03**	**0.54**	**0.04**	0.14	0.40		0.29	0.33	0.37	0.06	0.42	0.89
	Prange-s	0.39	0.45	0.38	**-0.79**	**0.27**	**0.00**	0.83	0.50	0.09	-0.05	0.41	0.89	-0.18	0.36	0.62	0.41	0.41	0.31
L-location	**Lopt**	**-1.37**	**0.44**	**0.00**	-0.46	0.31	0.12	0.22	0.49	0.66	-0.20	0.40	0.61	**-1.25**	**0.40**	**0.00**	-0.33	0.42	0.44
	Lmin	**-1.23**	**0.44**	**0.00**	0.15	0.28	0.58	-0.88	0.50	0.08	-0.07	0.38		-0.22	0.36	0.54	0.31	0.53	0.52
	Lmax	-0.73	0.44	0.10	-0.34	0.28	0.22	0.34	0.47	0.47	0.24	0.41	0.55	**0.82**	**0.37**	**0.02**	0.19	0.44	0.67
L-breadth	**Lsd**	0.41	0.44	0.35	-0.29	0.29	0.31	**1.17**	**0.45**	**0.01**	1.37	0.64		**0.67**	**0.37**	**0.08**	-0.36	0.41	
	AOO110	-0.06	0.44	0.90	-0.13	0.29	0.66	0.46	0.47	0.33	0.60	0.44		**1.06**	**0.35**	**0.00**	0.00	0.42	
	AOO11	-0.37	0.43	0.39	-0.07	0.29	0.80	0.28	0.47	0.55	0.37	0.41	0.36	**1.06**	**0.34**	**0.00**	-0.04	0.42	
	EOO110	-0.12	0.45	0.79	-0.48	0.28	0.09	**0.98**	**0.46**	**0.03**	1.58	0.76		0.43	0.36	0.24	0.02	0.43	
	EOO11	-0.14	0.45	0.75	-0.50	0.28	0.08	**0.97**	**0.46**	**0.04**	1.59	0.78		0.48	0.37	0.19	0.04	0.42	

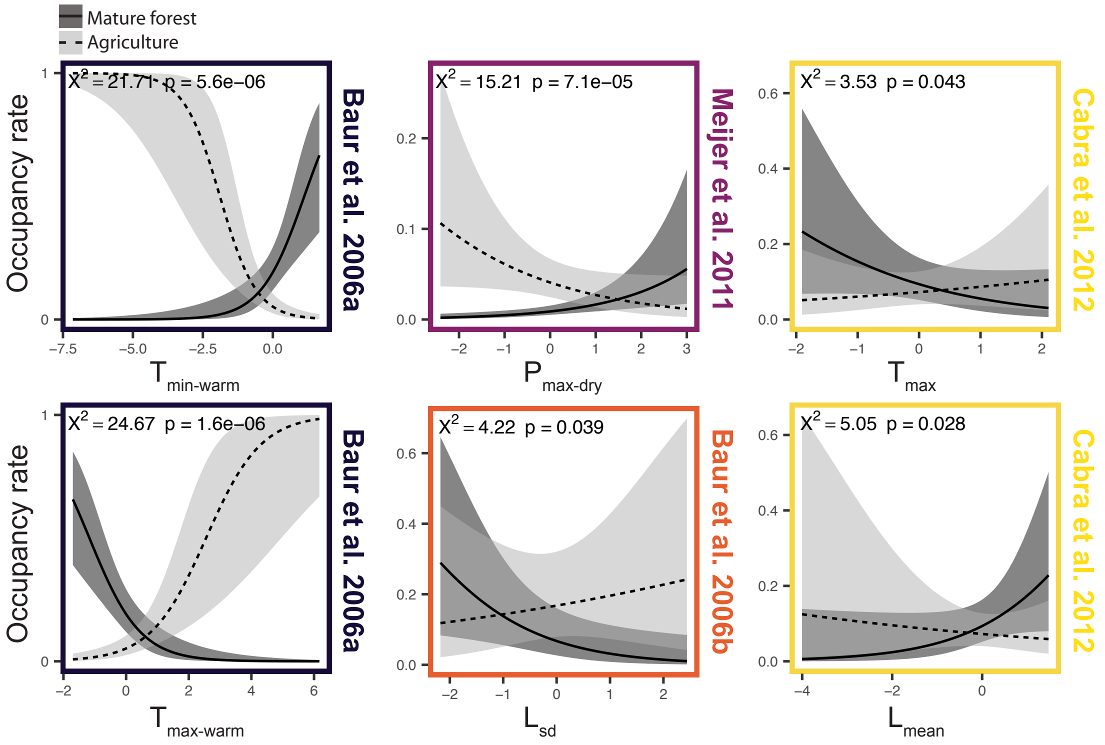

Figure 5.4 Fitted relationship for trait-environment interactions for each case study

Panel colours show each case study. X^2 values with 1-degree of freedom. *p*-values indicate significance of trait-environment interaction terms. Effects shown are marginal effects when all other geographic range and niche metrics are held at their mean values. Shaded regions are 95% confidence intervals. Note that non-significant terms in models with multiple trait-environment interactions are not shown, including whole case-studies with no significant trait-environment interactions (see Table 5.3).

5.5 Discussion

A wide-ranged ‘winners’ vs. narrow-ranged ‘losers’ pattern is emerging as a consistent response of local assemblages to habitat change (Cleary & Mooers, 2006; Scott *et al.*, 2006; Cofre *et al.*, 2007; Clavel *et al.*, 2011; Nowakowski *et al.*, 2017; Newbold *et al.*, 2018), but does not explain the mechanism whereby the winners win and losers lose. The results here suggest species’ environmental niches are at least part of the answer: providing better predictions of responses to land-use change than species’ geographic distributions in both global models and in four of six significant trait-environment interaction terms in independent case studies. Therefore, in other studies, the explanatory power of geographic ranges may arise from the correlation between wider environmental niche breadth, or wider physiological tolerances, enabling larger geographic range size (Slayter *et al.*, 2013; Kambach *et al.*, 2019) – a pattern supported in insects (Calosi *et al.*, 2010; Diamond & Chick, 2018). Environmental niche limits, if arising from environmental tolerance limits, also suggest a mechanistic link to land-use sensitivity. Overall, in this study of insect ectotherm sensitivity to land use, there is a detectable fingerprint of realised niches - but whether such a result holds for non-ectotherms remains uncertain. For instance, if geographic range size of endotherms are not driven by environmental tolerance limits, but instead by dispersal capacity or diet breadth then metrics of geographic ranges represent these mechanisms; in this case, geographic ranges may predict sensitivity to land-use better than realised niches (Newbold *et al.*, 2018).

Morphological and life-history traits mediate individuals’ interactions with abiotic environments. Variation in these traits among taxonomic groups reduces the prospect of finding general traits that predict species’ responses to environmental change. However, similarities in the biochemistry of life – i.e., demand for water, thermodynamics of protein functioning, thermal constraints to metabolic rates – mean that environmental tolerances, often mediated by physiology, are likely to strongly influence the limits of species’ realised niches (Corkrey *et al.*, 2012; Sunday *et al.*, 2012; Lee-Yaw *et al.*, 2016). The properties of environmental niche limits may therefore provide a generalisable predictive factor explaining species’ response to environmental change. Environmental niches simplify the complex issue of cross-taxon trait comparisons (Verberk *et al.*, 2013; Wong *et al.*, 2018), but the niche context dependencies identified here suggests a major challenge remains in understanding which of many multi-dimensional niches axes are most relevant.

We demonstrate that the effects of environmental niche limits on species' responses to land-use change may be highly context-dependent, through performing sensitivity analyses and examining independent case studies. The variation in context-dependency may have been relegated to the model's random terms by simply quantifying a global response to land-use change. Thermal niches, precipitation niches, and sometimes geographic range effects, are all supported depending on the case-study examined. Identifying the causes of these context-dependency was not possible, but multiple factors may be at play even though I study a well-established directional microclimatic change. First, even if species were to respond only to their abiotic environment; local temperature, water availability, and humidity change simultaneously leading to complex observed responses. Second, responses can interact amongst abiotic stressors, for example, individual thermal tolerances depend on the variability in precipitation and temperature experience by the source population (Clusella-Trullas *et al.*, 2011; Kellermann *et al.*, 2012). Finally, species' abiotic responses will also affect other species in the system (i.e., responses seen in our data will reflect effects of biotic as well as abiotic environmental changes). Niche context-dependency is also apparent in field studies of different insect groups; for example, temperature is important for ants (Kaspari *et al.*, 2015; Boyle *et al.* in review) but humidity and desiccation tolerance may be more important for termites (Chung *et al.*, 2018). Here, night-flying Lepidoptera have the strongest thermal niche by land-use interaction, for both warm and cool thermal limits, perhaps suggesting limited mid-day behavioural thermoregulation, and an important role of night-time temperatures for activity in this group, which warrant further investigation. The other case studies have less obvious regional or taxonomic drivers of context-dependencies; future work should attempt to identify the nature of context-dependent effects to better ascertain when and why certain niche dimensions are important.

I interpret the significant trait-environment interactions as a signal of environmental filtering; overall, microclimatic filtering effect on occupancy and abundance may be a general principle in ectotherm responses to land-use change (Andersen, 2018). For example, I find evidence that the local warming of habitats due to conversion of mature forest selects for species based on their thermal niche. A new study of 50 ant species in Borneo provides direct evidence for the link between land use, temperature change and critical thermal limits which determined species' abundance responses (Boyle *et al.* in review). Ant species' responses to the conversion of primary forest to oil-palm plantation (a 5.6°C shift in microclimate) depended on their critical upper limits, with a 1°C increase in critical upper limits resulting in a 23.3% increase in abundance in plantations relative to primary forest (Boyle *et al.* in review). Furthermore, insects appear to adapt life-history traits to temperatures in different land uses, implying that temperature differences between habitats result in fitness differences that underpin environmental filtering (Karlsson & Wiklund, 2005). In reptiles and amphibians, critical thermal limits explain ~40% variation in species' abundance responses to land-use change (Nowakowski *et al.*, 2018).

The importance of local environmental niche filtering suggests that the response diversity of the regional assemblage, in terms of the diversity of environmental responses, may influence land-use change affects local richness and community composition (Elmqvist *et al.*, 2003). The role of regional environmental niche diversity in facilitating or moderating shifts of biodiversity and ecosystem function may be greatly underappreciated (e.g., Dee *et al.* 2016, Garcia *et al.* 2018; Chapter 4). The traits and niches of regional native species pools are important in understanding the 'winners' and 'losers' of biodiversity change (Tabarelli *et al.*, 2012; McCune & Vellend, 2013). For example, if the regional species pool is a mix of warm and cool tolerant species then local richness will be maintained by the local turnover of species identity with land-use change. Alternatively, if there is little thermal diversity in the regional pool then cool-affinity species cannot be replaced by warm-affinity species and richness is lost with land-use change (e.g., ecological or biogeographic constraints limit community re-assembly, Bertrand *et al.*, 2016). Regional thermal response diversity may be a potential mechanism facilitating assemblage change; for example, high topographic heterogeneity (linked to thermal heterogeneity) correlated with stronger assemblage re-organisation after an extreme drought event in UK butterfly assemblages (De Palma *et al.*, 2017). Spatial management of topographically complex regions is recognised as a tool in mitigating the ecological impacts of climate warming (Heller & Zavaleta, 2009); assemblage reorganisation to land-use changes that modify microclimates may therefore depend on topographic complexity (Oliver *et al.*, 2010; Lenoir *et al.*, 2013; Katayama *et al.*, 2014) and open space management (Smith *et al.*, 2007).

Two strong caveats must be acknowledged in interpreting our results. First, I quantify realised niches without considering their mechanistic basis and simply correlate occurrence to environmental variables. Second, there is a substantial difference in spatial scale between niche limits defined from large-scale climate gradients with the small-scale microenvironments that insects experience (see Chapter 6). A single leaf can have a larger thermal gradient than average climates spanning hundreds of kilometres of latitude (Pincebourde & Woods, 2012; Pincebourde *et al.*, 2016). Sources of microclimate variation are an important driver of ecological processes, facilitating behavioural thermoregulation, space-use, and thermal niche partitioning (e.g., Kaspari *et al.*, 2015). However, the potential for microclimate variation, and the extremes of this variation, is constrained by the broader climate a habitat is within (Graae *et al.*, 2012), and individuals and populations often move within and experience this larger scale climate variability as a whole (Sears *et al.*, 2011, 2016). As such, the use of climate gradients to estimate species' realised niches can still be *predictive* – but incorporating finer-scale variation defining realised niche limits may improve this predictive.

In addition, the decision to bundle multiple agricultural practises into a single factor may add to the heterogeneous picture presented here; but was a necessary limitation to simplify models. Niche effects may be less important in transitions to secondary forest which have less extreme microclimatic shifts (Senior *et al.*, 2017, 2018). By necessity my results are biased towards relatively common species that have available species' occurrence data. Distribution metrics may be less predictive in rare species for which range limits may be strongly limited by processes such as dispersal limitation, species' interactions and habitat availability.

Nonetheless, simple predictive metrics of species' sensitivity to environmental change are needed, given the data paucity researchers face for the vast majority of biodiversity (Ballesteros-Mejia *et al.*, 2013; Faith *et al.*, 2013; Amano *et al.*, 2016). Realised niches have the benefit of estimating niche properties for whole assemblages of species, which remains a considerable challenge for direct thermal tolerances measures (but see Bates *et al.*, 2010, Boyle *et al.* in review). Large-scale distribution data may be imperfect, but this analysis demonstrates their use to help predict species' response to land-use change. This work suggests niche properties derived from species' distributions appear to be a simple but relatively predictive tool that could be estimated for many thousands of species from GBIF's freely available data.

5.6 Literature cited

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Chapter 6 Discussion

6.1 Abstract

The motivation for this thesis was to describe patterns in species' realised niches and thermal heterogeneity to build the requisite knowledge to describe and predict assemblage scale responses to climatic warming. This chapter first provides an overview of the main findings. I next synthesise insights across chapters in the context of compositional turnover, the context-dependency of niche effects and methodological approaches in terms of data and statistics used throughout. Two themes are further discussed: i) the realisation of fundamental niches in geographic space, and how such realisation can limit quantifying and predicting biodiversity change; ii) the organismal, spatial, and temporal scales of realised niches. Finally, I discuss the relevance of the results presented in this thesis for informing biodiversity management in the context of climate change.

6.2 Overview

In Chapter 2 (Waldock *et al.*, 2018), I investigated how the signatures of temperature change occur in space and time. I asked what role do these spatial and temporal dimensions of temperature change have in driving changes in species richness, the turnover of species identities and changing composition of local assemblages? And, how are well are these effects represented in the literature? I found that assemblage scale studies focus mean temperature change – but temperature change is multi-dimensional. I argue that these dimensions are nonetheless important to consider. For example, multiple temperature-change pathways can lead to community homogenisation and species richness change – important Anthropocene biodiversity change signals outlined in Chapter 1. As such, I provide a framework that helps link biodiversity drivers and responses in specific dimensions of space and time. This literature review also revealed that how local abundance relates to temperature may be important, to improve our prediction of ecological responses to climate warming. In addition, the local diversity in species niches was often implied as an important feature determining an assemblage's response to temperature change, but was rarely considered. The next chapters of my thesis explored these themes in shallow-water reef fishes.

In Chapter 3 (Waldock *et al.*, 2019), I quantified how abundance varied across species thermal ranges, a measure of species' thermal niche structure. I found that, on average, maximum abundance strongly related to sea surface temperatures. These abundance-distributions were often non-linear with peaks near the centre of species' thermal ranges. This work provides strong support for the 'abundance-centre' hypothesis, a long-standing macroecological theory that has remained challenging to test convincingly to date. However, a great deal of variability occurred in species' abundance-distributions despite a broadly predictably pattern at larger scales; this result was surprising as temperature is often asserted to be a highly explanatory factor limiting species' distributions (see 6.4). This variability manifested within species as a high amount of scatter of local abundance below thermal-abundance curves defined by maximum abundance; between species I identified a variability in thermal niche skew defining a distinct pattern from the tropics to temperate regions. This diversity of thermal niches may filter to local assemblages which may be important to consider in how assemblages respond to climate events.

In Chapter 4, I quantified responses diversity of local assemblages and simulated local responses to heatwave events. The first aim of Chapter 4 was to investigate spatial patterns in response diversity in the Great Barrier Reef and western Coral Sea system. I applied a 'model-based' approach to response diversity which is novel in quantifying species responses to environmental gradients directly for local and regional scales at the same time. The result of doing so revealed two potential mechanisms of resilience. First, I found that many herbivore groups had spatially homogenous patterns of response diversity. Second, some functional groups had a similar level of regional and local response diversity. The second aim of this chapter was to tease apart the effects of simultaneous environmental changes in natural and simulated warming events. When singled out, warming predicted an average increase in occupancy rates across all functional groups, matching the frequently observed warm-skew in abundance-distributions of tropical fishes from Chapter 3 (Waldock *et al.*, 2019). A surprise in this chapter were that herbivores were, on average, insensitive to changes in algae cover a finding perhaps underpinned by response diversity; and, that coral cover only strongly influenced the functional groups that feed on coral structures.

In Chapter 5 I broaden my perspective to consider if thermal and precipitation realised niches explain occurrence of species amongst land-use types. I found that thermal and precipitation niche limits influenced occupancy of different land-uses and these patterns consistently matched the expected microclimatic environmental changes with changes from forest to agricultural land uses. However, results were surprisingly context-dependent in that the most predictive niche dimensions varied amongst studies (see 6.3). Therefore, niches may not provide simple predictive tools (see 6.4). The clarity of niche effects may have been influenced by factors such as coarse-scale distribution data, heterogeneous land-use comparisons, and behavioural regulation in fine-scale microhabitats.

6.3 Synthesis

Looking across the chapters presented here provides insights to assemblage compositional change outlined in the introduction of this thesis as a characteristic response to Anthropogenic pressures. For example, in Chapter 5 insect species responses to land-use change depended on species' realised thermal niches, such that the changing species' assemblage composition is towards species with warmer affinities (Barnagaud *et al.*, 2013; Frishkoff *et al.*, 2016). In addition, abundance was structured across species' realised thermal niches in Chapter 3. Therefore, compositional shifts in local assemblage composition could occur with warming with no range shifts: abundance change may contribute to compositional turnover through species turnover in maximum abundance with warming. In Chapter 4, a diversity of responses to temperature within functional groups was identified at the sub-assemblage level. Therefore, species that provide unique ecological roles within assemblages, i.e., functional groups, may shift in composition with warming. Together, these results imply that multiple pathways contribute to the compositional turnover of assemblages. Outlined in Chapter 2 are the temperature-change dimensions that can result in different patterns of compositional turnover through species' range shifts and abundance changes.

Context-dependent assemblage responses to warming are implied throughout this thesis. Context-dependent effects could be defined as different responses of two assemblages to the same magnitude of warming. Chapter 2 suggests that context-dependent effects may arise where two assemblages are exposed to the same mean temperature change but through different spatial and temporal dimensions. The variation underneath the 'curved-ceiling' of maximum abundance in Chapter 3 – despite the use of multiple regressions that should account for multiple sources of variation – implies that local unobserved effects strongly influence a species' abundance at a given site (i.e., historic effects, population stochasticity, local interactions, recruitment events). Thus, if temperature is not limiting abundance locally, the capacity for temperature change affect abundance may depend on such local context-dependencies. In addition, the non-linearity in realised niches in Chapter 3 suggests that abundance responses depend on the thermal niche context of local assemblages, i.e., local temperature relative to the features of a species' realised niche. A capacity for further context-dependencies is suggested by Chapter 4: if assemblages exist in a network of sites that have high response diversity, then responses can be replenished through species movements. Thus, changes to future ecosystem functions may need to be considered in the context of the response diversity of the regional species pool. Furthermore, the simulations in Chapter 4 identify that functional group responses to a single heatwave event can be determined by multiple stressors, that can have opposite effects. The overall ecosystem functioning is highly context-dependent because different groups have different responses to each environmental change during a heatwave. Furthermore, if each environmental change during a heatwave differs in magnitude (i.e., warming with no coral loss; coral loss but no algae gains) then the overall ecological responses are further complicated. Finally, different realised niches were important between studies in Chapter 5 and so realised niches dimensions were likely to be dependent on the specific studies context of taxonomic groups, regions and agricultural practises. Overall, such context-dependencies may limit the simple predictive power of realised niches (see 6.4)

The analyses in this thesis depended on the availability of data that characterise species distributions (Meyer *et al.*, 2015; Amano *et al.*, 2016; Edgar *et al.*, 2016) and documents biodiversity change (Hudson *et al.*, 2017; Dornelas *et al.*, 2018; Pagad *et al.*, 2018). However, bias, heterogeneity and under-sampling are prevalent in occurrence (Ballesteros-Mejia *et al.*, 2013; Meyer *et al.*, 2015) and biodiversity change data (Magurran *et al.*, 2010; Gonzalez *et al.*, 2016). Stasis in the temporal and spatial scale of ecological study over the last decade implicates practical (i.e., man-power) and societal (i.e., funding distribution, global inequality) constraints on resolving these data issues. Such challenges are notable at an assemblage scale because data limitations can also vary between species. Promising initiatives, capitalized on throughout this thesis, include standardised high-quality citizen-science datasets in Chapters 3 and 4 (Sauer *et al.*, 2013; Edgar & Stuart-Smith, 2014) and globally representative data syntheses in Chapter 5 (Hudson *et al.*, 2017). These approaches helped overcome data constraints to establish thermal niche patterns at an assemblage scale. Further efforts to synthesis available biodiversity data are important to generalise biodiversity patterns and responses at scales larger than a single study (e.g., Dornelas *et al.*, 2018). However, data limitations are likely endure, justifying development of clearer theory on biodiversity change to make explicit anticipatory predictions (e.g., Chapter 2; Azaele *et al.* 2015, Chase *et al.* 2018). In addition, applying newly developed statistical approaches to estimate realised species niches is necessary for accurate inferences to be made from limited available data (e.g., Beale and Lennon 2012) – applying emerging statistical tools in each chapter of this thesis has enable greater insights than the application of more traditional methods. For example, in Chapter 3 I used a recently developed quantile approach to additive modelling (Fasiolo *et al.*, 2017): combining the benefits of flexible modelling approaches and quantile regression, which help test how abiotic factors limit abundance despite highly context-dependent and local effects that cause abundance to fluctuate widely between similar sites (Cade & Noon, 2003; Austin, 2007). Whilst non-linearities could have been incorporated with quadratic terms, such models are less flexible and may have missed the skewed distributions identified (Chapter 3; Waldock *et al.* 2019). In addition, Chapter 4 applies the HMSC statistical framework to quantify response diversity which helped to directly scale from species niches (i.e., realised niches) to assemblage patterns (Ovaskainen *et al.*, 2017) – amongst many benefits, doing so also allowed the comparison between regional and local response diversity patterns.

6.4 Realised thermal niches and predicting ecological change

Throughout this thesis, I found that spatial environmental gradients in temperature influenced species abundance and occupancy (Waldock *et al.*, 2019; Chapter 4; Chapter 5). Temperature effects were present in both marine and terrestrial systems and at local (i.e., land-use gradients) to global scales (e.g., Chapter 3 & 4 vs. Chapter 5). Here, I investigated temperature as a model environmental axis (Beaugrand, 2014a). This choice is well justified because temperature has many important direct effect on organisms, as evidenced from: the temperature dependence of metabolic (Gillooly *et al.*, 2001; Brown *et al.*, 2004) and biological rates (Dell *et al.*, 2011), well-defined thermal limits to species performance (Angilletta, 2009; Sunday *et al.*, 2011), strong behavioural selection of optimal temperatures (Bates *et al.*, 2010), tolerance limits that often match geographic range limits (Lee-Yaw *et al.*, 2016) leading to species' range and phenological shifts with environmental warming (Parmesan & Yohe, 2003; Thackeray *et al.*, 2010; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013). Therefore, temperature appears an important environmental variable to estimate climate changes effects at multiple biological scales. Indeed, a 'Macroecological Theory of All Life' (METAL) has been developed to explain biodiversity dynamics largely through variation in the position and breadth of species thermal niches alone (Beaugrand, 2014b; Beaugrand *et al.*, 2019).

The above view is limited if species fundamental niches are not the main factor constraining species realised distributions. Realised niche breadth is often smaller than fundamental niche breadth which suggests distributions are frequently limited by factors other than abiotic environmental limits (Soberón & Arroyo-Peña, 2017). For example, the native ranges of invasive species can be constrained by conspecifics, the invasive range can be outside the realised niche and would not have been predicted as tolerable based on the native realised environmental conditions (Tingley *et al.*, 2014). Despite temperature often being the most important variable in my analyses, I also found that local factors and other sources of abiotic variation act in concert with temperature. Therefore, realised niches defined from species niches in this thesis are not only constrained by fundamental niches. That realised niches are influenced by more than just temperature throughout this thesis is supported by: the high proportion of unexplained variation in maximum abundance within species in Chapter 3; in Chapter 4, measured and unmeasured variables together contributed to ~50% of the total explained variation, in addition to sea-surface temperature; and, there was high context dependence of different niche dimensions in Chapter 5. More widely, the relative importance of temperature structuring realised niches varies substantially amongst endotherms and ectotherms (Sunday *et al.*, 2011; Khaliq *et al.*, 2014); amongst organisms that inhabit environments with different amounts of thermal variability (Steele *et al.*, 2018); amongst organisms that interact with their environments at different spatial and temporal scales (Holling, 1992; Pincebourde & Casas, 2019); furthermore, individual thermal niches also interact with broad scale climates such that temperature effects can be context dependent (Clusella-Trullas *et al.*, 2011), and temperature can alter species' interactions leading to further complexities (Ockendon *et al.*, 2014).

Therefore, the predictive capacity of the thermal niches considered in this thesis, to explain temperature-driven biodiversity change, depends strongly on how well the fundamental niches of species in local assemblages are realised in geographic space (Soberón & Nakamura, 2009; Soberón & Arroyo-Peña, 2017). Factors that influence the filtering of fundamental niches to realised distributions induce uncertainty when describing biodiversity change from realised thermal niches alone (Figure 6.1; e.g., disperal limitaitons, climate variability and range disequilibrium, geographic barriers; Early and Sax 2011). As such, multiple challenges remain for accurate prediction of local assemblage dynamics from realised thermal niches (Mouquet *et al.* 2015; Blonder *et al.* 2017). One challenge identified in Chapter 3 and 4 of this thesis is the existence of variation in the shape species niches and the varied distribution of niches between species (i.e., uneven spread of thermal range limits in Chapter 3), within regional species pools. This realised niche diversity has been shown to induce complex community

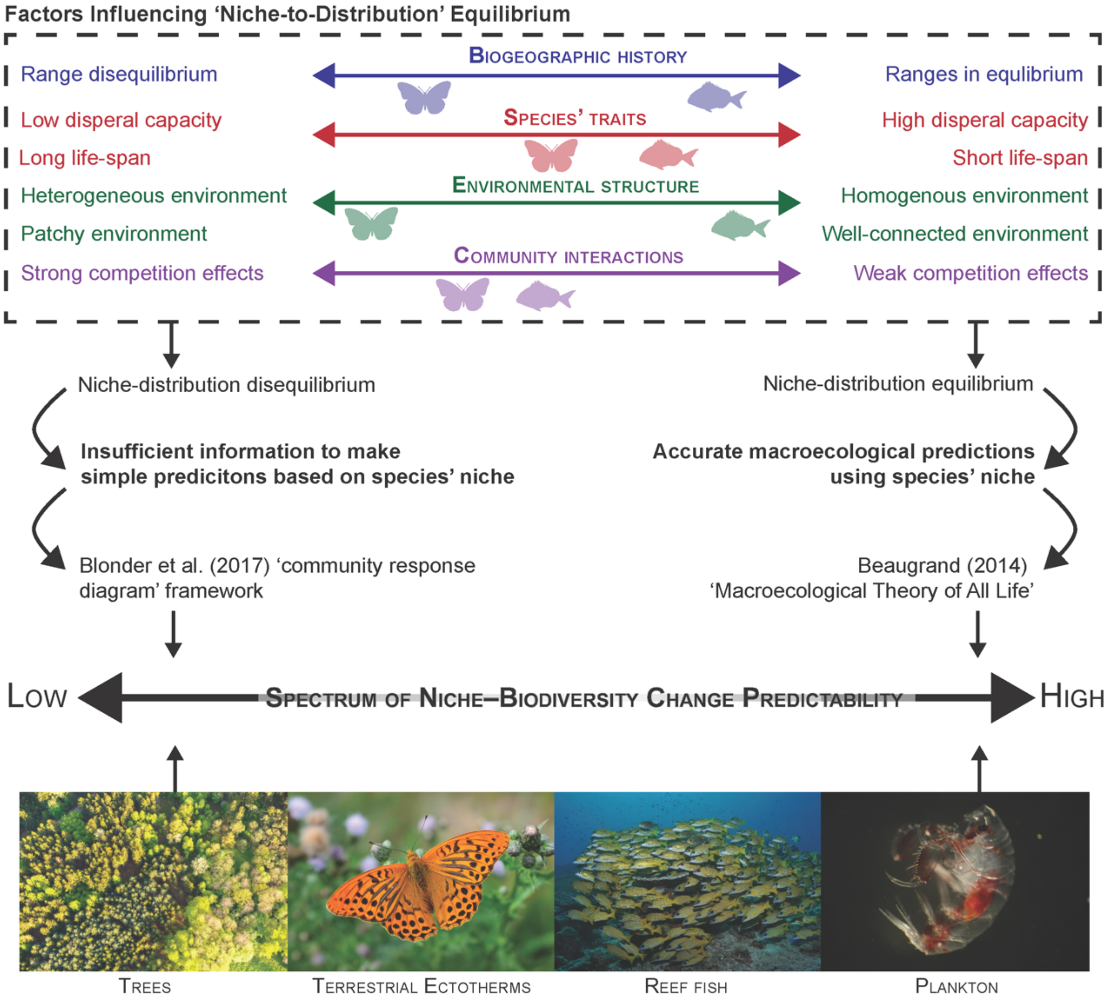

Figure 6.1 Factors that influence how well species' fundamental niches represent species' realised niches via species' distributions, and the consequences for predicting biodiversity change. The predictability largely depends on whether species distributions are in equilibrium with the environment and can maintain this equilibrium, and thus whether realised niches match fundamental niches. The capacity to track environmental change often determines this equilibrium (i.e., dispersal capacity, dispersal barriers). This predictability is linked to two methodological and conceptual frameworks which both centre around the species niche, as discussed in the main text. Example ectotherm taxonomic groups are placed along this spectrum, as well as the key taxonomic groups of focus in this thesis as represented by symbols in the top panel.

dynamics (Blonder *et al.*, 2017) that can be lagged behind temperature changes (Devictor *et al.*, 2012; La Sorte & Jetz, 2012; Gaüzère *et al.*, 2018).

The niche concept has therefore provided both accurate (Beaugrand *et al.*, 2019) and inaccurate (Blonder *et al.*, 2017; Gaüzère *et al.*, 2018) predictions of community dynamics – a dichotomy that should be resolved. A comparison of the ecological systems these theories and methodological tools are developed within may help (Figure 6.1). I suggest that spectrum exists in whether observed (i.e., realised) species distributions and abundance accurately measure a species response to abiotic environments alone – and therefore in the predictability of assemblage dynamics from realised niches. Many factors contribute to this disparity in realised from fundamental niches which vary among realms ecosystems, environments, and taxonomic groups (Sunday *et al.*, 2012). Such differences in alignment on spectrum may have led to contrasting predictive frameworks from similar starting principals. For example, predicting reef fish responses to temperature change from the realised niches in Chapters 3 and 4 may be better justified (Bates *et al.*, 2014; Booth *et al.*, 2018; Day *et al.*, 2018) than the insect groups considered in Chapter 5, which may further explain the variable and context-dependent niche effects (Figure 6.1). The cross-system comparison in this thesis suggests that future research should address: Which ecological systems have little or no predictability as species realised niches always poorly represent species fundamental niches? Which factors have largest effect on predictability, due to the disequilibrium of fundamental from realised niches (e.g., competition vs. dispersal)? And, how do different taxonomic assemblages and ecosystems align along this spectrum (and how can these be quantified and compared)? If the majority of biodiversity falls within unpredictable ecosystems we may have to re-evaluate our expectations of management decisions and policy actions by accepting high uncertainty (Schindler & Hilborn, 2015), develop better methodological and conceptual frameworks (Petchey *et al.*, 2015; Dietze, 2017) and reprioritise predictions of ecological dynamics to only particular systems (Beaugrand, 2014a; Yates *et al.*, 2018).

6.5 Biological, spatial, and temporal scale of the niche

> "*Generally, when we attempt to move from larger, more inclusive scales to smaller ones, we should be looking at how processes at the larger scale constrain the smaller ones. Conversely, when we attempt to move from smaller to larger scales, we should be attempting to show how processes at the smaller scales determine the statistical properties of entities at larger scales. The mode*

> *of explanation is different in each case. In the former, we look for boundaries or types of processes that cannot occur. In the latter, we attempt something akin to classical statistical mechanics: we try to show how complexity at the lower scale leads to regularities at the higher scale.*" – Maurer, 1999.

It is important to consider the assumptions made throughout this thesis in estimating species responses to environmental gradients at large spatial scales. The niche defined at a species-level is unrealistic because natural selection acts to determine the fitness of individuals, and the individual is the biological unit that interacts with thermal environments (Huey *et al.*, 2012). This smaller scale of individuals, and not species, implicates fine-scale thermal heterogeneity in both spatial (Otero *et al.*, 2015; Barton *et al.*, 2019) and temporal (Tracy & Christian, 1986; Trudgill *et al.*, 2005; Sheldon & Dillon, 2016) dimensions as key determinants of an individual's performance. Thus, it could be argued that quantifying temperatures effect on population abundance and species' distributions depends first on the measuring the how temperature influences individuals fitness (Pörtner, 2001; Holt, 2009; Kearney & Porter, 2009; Kearney *et al.*, 2010; Chown, 2012; Huey *et al.*, 2012). Whilst this mechanistic individual view is more accurate in terms of evolutionary processes driving fitness, it is often impractical to apply generally, apart from in particular focal species (Stoffels *et al.*, 2016; Barton *et al.*, 2019).

Estimating niches at the individual and species scales (as considered in here) have similar goals and limitations. The goal is to approximate individuals' fitness across an environmental gradient (Holt, 2009). A shared limitation is the inadequacy of metrics at individual and species level to represent individuals' fitness (Sinclair *et al.*, 2016; Gvoždík, 2018). For example, at an individual scale, measurable thermal performance traits (e.g., sprint speed, habitat selection, heart rate) relate only loosely to fitness (Huey *et al.*, 2012; Sinclair *et al.*, 2016). For populations, the measurement of demographic rates may imperfectly relate to fitness due to factors such as life-history trade-offs (Holt, 2009; Thompson *et al.*, 2017). At a species scale I focus on 'ecological performance' metrics. For example, Chapter 3 considers abundance and Chapters 4 and 5 consider occurrence. These metrics are used as proxies for an average of all individuals fitness at a local site with the assumption that individual fitness averages to scale up to affect local abundance and probability of occurrence. Such metrics have the benefit of being highly relevant for ecological processes despite this assumption. Yet, these observational ecological measures imperfectly relate to fitness. The observation of a high number of individuals does not mean that those individuals will contribute strongly to the genetic composition in the future due to source-sink population dynamics, extinction debts and individual aggregations effects that might lead to fitness being over- or under-estimated (Jackson & Sax, 2010).

An additional challenge in defining niches is accurately representing the spatial and temporal scale that individuals, populations, and species experience and interact with their environment and environmental heterogeneity (Wiens, 1989; Holling, 1992; Levin, 1992; Holland *et al.*, 2004). Species intrinsically vary in the spatial scale that individuals interact with their environment (e.g., home range size) or that species are distributed across the environment (e.g., geographic range size; Gaston & Blackburn 1996, Jetz *et al.* 2004, Tamburello *et al.* 2015). Species also have intrinsic temporal scales to their life-cycle and phenology (Lindstedt & Calder, 1981; Moss *et al.*, 2016). These multiple intrinsic factors interact with the extrinsic spatial and temporal dimensions of temperature (as in Chapter 2), such as microclimates, diurnal variability and patterns in climate variability (e.g., El Nino). The predictive ability of niche estimates depends, to a large extent, on how well these intrinsic factors match the extrinsic scales used to quantify species' realised niches (Randin *et al.*, 2009; Sears *et al.*, 2011, 2016; Yates *et al.*, 2018), as does the accuracy of climate change impact assessments for species (Nadeau *et al.*, 2017). However, opinions differ about which biological scales (i.e., intrinsic) should be considered. For example, Potter *et al.* (2013) argue against using species distribution models because environmental data are often 10,000-fold the body size of the organism they model – implying that only the environment surrounding an organism is important (also see Pincebourde and Casas 2019). In contrast, Nadeau *et al.* (2017) consider the area that population dynamics operate as important, rather than individuals, and suggest that the scale of environmental data match to biologically relevant scales for bird and large mammals but not small mammals, herpetofauna and plants.

Considering the processes that structure realised niches at multiple scales may be more informative that choosing between particular scales (Levin, 1992; Potochnik & McGill, 2012). That only large-scales covariates are often considered in correlative models may explain, in part, the limited transferability of SDMs to new time periods or environmental conditions (Eskildsen *et al.*, 2013; Regos *et al.*, 2019). However, models built from coarse environmental data can sometimes have good predictive ability in new time frames (Dobrowski *et al.*, 2011; Johnston *et al.*, 2013) which suggests coarse-scale niche estimates sometimes capture important processes.

The transferability of models, including biophysical and species distribution models, to new conditions (e.g., time-frame, novel climates, unmonitored locations) is an emerging field (Sequeira *et al.*, 2018; Yates *et al.*, 2018); improving model predictability is key to building more transferable models (Yates *et al.*, 2018). Predictability of correlative models for assemblages may be improved by matching the multi-scale nature of species niches and their abiotic environments (Mertes & Jetz, 2018; Graham *et al.*, 2019). At present, most multi-scale considerations in niche models attempt to integrate fine-scale land-use and habitat data with large-scale climate estimates (Pearson *et al.*, 2004; Bellamy *et al.*, 2013; Bradter *et al.*, 2013; Graham *et al.*, 2019). Yet, the fine-scale influence of microclimates are less well considered alongside large-scale climate data (Barton *et al.*, 2019); microclimates are intricately related to land-use change too which further complicates matters (Senior *et al.*, 2017; De Frenne *et al.*, 2019). Furthermore, is not obvious that resolving the temporal and spatial domains in more detail (i.e., months to hours, kilometres to millimetres) will always, or indefinitely, improve predictive power. For example, the prediction of sessile organisms may improve using fine-scale data because the environment experienced by individuals is better represented (Franklin *et al.*, 2013; Manzoor *et al.*, 2018; Mertes & Jetz, 2018). But, predictive power may decrease for mobile individuals when matching coarse point occurrences (e.g., GBIF) to well-resolved climate data in space and time. Niches defined from distributions may always perform poorly where species are extremely mobile and track dynamic environments (e.g., pelagic predators; Block *et al.* 2011), where tracking organisms directly is more informative (e.g., McMahon & Hays 2006, Payne *et al.* 2016, Scales *et al.* 2017). For example, in this thesis I aggregate sea-surface temperature from daily records to >yearly records to better represent how temperature regulates populations and occurrences in Chapters 3 and 4. In Chapter 5, monthly seasonal temperatures were more predictive that yearly averages which may suggest the temporal scale and time period most relevant to regulate species occurrence patterns (i.e., temperatures during life-cycle stages).

Multi-scale environmental covariates may help to capture the separate temperature-related processes at fine and coarse scales that influence individual, population and species performance (Levin, 1992). I propose that a multi-scale approach could use macroecological scaling rules between body size and home-range size to gather relevant spatial domains of individuals (Jetz *et al.*, 2004; Tamburello *et al.*, 2015). Home-range size provides the individual scale that organisms interact with their environment, and this spatial scale could be applied as a buffer to point-occurrences. Fine-scale climate data inside this buffer could help estimate properties of the environment that individuals to operate within, for example: the area of microclimates available; amount of thermal heterogeneity for behavioural regulation; the amount of activity-time available in a day; or, the location of nearby microclimates for local range shifts. As such, multiple dimensions of temperature may be important for defining niches as they are for assemblage dynamics as outlined in Chapter 2 (e.g., Sears *et al.* 2016, Barton *et al.* 2019). Thus, the effect of fine-scale mechanisms could also be captured by correlative modelling, based on macroecological principals, combined with increasingly high-resolution environmental data. Coarser-scale climates may still be useful to represent the processes that regulate populations and meta-populations (Bellamy *et al.*, 2013). Model selection amongst multi-scale covariates could inform which biological scales constrain species' distributions and thereby structure realised niches (Holland *et al.*, 2004). Such an approach would benefit from: algorithms and software to down-scale climate data (e.g., Storlie *et al.* 2014, Kearney & Porter 2017); development of multi-scale environmental metrics (Graham *et al.*, 2019); standardised methods to optimise niche model structure amongst multi-scale environmental metrics (Manzoor *et al.*, 2018; Mertes & Jetz, 2018); and, data infrastructure to integrate space-use of individuals and populations with point-occurrence data.

6.6 Species niches in the regional pool: a conundrum for conservation in a changing climate

Management actions can help retain functioning ecosystems that resist, or facilitate, biodiversity change with climate change (Heller & Zavaleta, 2009; Mawdsley *et al.*, 2009; Jones *et al.*, 2016). Climate effects multiple species across large spatial scales (Heller & Zavaleta, 2009). A regional scale approach to policy and planning is necessary. In this thesis, I investigate broad spatial scales and species assemblages, therefore some insights from this work may be relevant in the context of climate adaptation (explored in Table 6.1). A regional and biogeographic perspective to management is necessary because the spatial scales of species' distributions are far larger than most protected areas – or quotas defined at national scales – and species may have to move over large regions to maintain climate equilibrium in the future (e.g., 60% European protected areas are <10km^2, source: www.eea.europa.eu). Managing for ecological integrity at this larger scale is important but challenging (e.g., Chester *et al.* 2012). At present, protected areas are not biased towards slower warming areas that could act as refugia (Bruno *et al.*, 2018); are too small as networks to contain full species' ranges (Fredston-Hermann *et al.*,

Table 6.1 Climate-change management actions. Key actions groups are identified in (black rows). Left column is actions identified through literature reviews. Right column shows relevant results from this thesis. Key actions and agendas groups are identified from Heller & Zavaleta (2009), Mawdsley *et al.* (2009) and Jones *et al.* (2016). (Note that bullet points in left and right columns do not relate.)

Actions and research agendas	Thesis contributions (Chapter)
Accept uncertainty, complex responses, and surprises	
• Identify sources of prediction error (Thuiller *et al.*, 2019). • Better predict outcomes of novel species interactions (Alexander *et al.*, 2015). • Quantify the effect of non-linearities in biological responses. • Better account for multiple scales and dimensions of climate change (Garcia *et al.*, 2014; Brito-Morales *et al.*, 2018). • Make plans flexible to incorporate new knowledge. • Avoid rigidity in physical conservation infrastructure.	• Assemblages response to multiple dimensions of climate change that may co-occur (2). • High variability in abundance suggest low local-scale predictability (3). • Non-linear biotic responses (3) that vary amongst species and functional groups (3, 4) leads to high uncertainty in species responses. • Different relative importance of abiotic and biotic environmental changes (4). • Niche axes show context-dependent responses (5).
Define and protect climate refugia	
• Identify areas where climate change will have little impact (Levy & Ban, 2013) and are intact (Eigenbrod *et al.*, 2015). • Identify areas where species distributions will converge (Loyola *et al.*, 2013). • Identify historic refugia during past climate changes (Millar & Brubaker, 2001). • Identify topographically complex regions (Schloss *et al.*, 2011).	• Skewed distributions in tropics suggests this region lacks refugia and is sensitive (3). • Areas of high response diversity exist where ecosystem function will be maintained (4).
Decrease biogeographic barriers and facilitate dispersal	
• Increase landscape connectivity so species can track climate change (Game *et al.*, 2011). • Latitudinally arrange reserves (Fredston-Hermann *et al.*, 2018). • Decrease matrix hostility and increase landscape permeability (Theobald *et al.*, 2012). • Increase reserve size and connectedness (Green *et al.*, 2015). • Organise reserve networks between nations and jurisdictions (Chester *et al.*, 2012).	• Sub-tropical transition exists in realised niches (3) that may contribute to biotic lags and complex responses. • Species capacity to range shift through agricultural land-use depends on niche effects (5). • Hostility of agricultural land-use to range shifts may be context dependent (5).
Protect heterogeneity	
• Select regions with high abiotic and bioclimatic diversity (Ackerly *et al.*, 2010). • Identify topographically complex regions with low climate velocity (Schloss *et al.*, 2011). • Conserve the ‘stage’ for biodiversity change ‘actors’ (Lawler *et al.*, 2015).	• Response diversity is a form of biotic heterogeneity. Identifying regions of high response diversity may be important for maintaining ecological function (4).

Deemphasise historic baselines and focus on retaining ecological processes and functions	
• Embrace changing species' compositions but retain ecological functions (Harris *et al.*, 2006). • Focus efforts on assemblage and ecosystem scale rather than retaining particular species (McLeod *et al.*, 2009).	• Maintenance of ecosystem function may be predicted through quantifying functional group response diversity (4).
Consider interactions between land-use and climate change	
• Consider effect of changes in land-use arrangement and intensity in ability to respond to climate (Nuñez *et al.*, 2013). • Consider combined effects of land-use and climate change (Newbold, 2018). • Reduce land-use intensity which can prevent community reorganisation during warming (Oliver *et al.*, 2017). • Identify the capacity for land-use change to prime environments for, and benefit, range shifting species (Guo *et al.*, 2018).	• Benefits of land-use for warm affinity species suggests potential environmental priming for range shifts (5). • Topographic complexity that increases regional abiotic heterogeneity may facilitate responses to land-use change and climate change (5).

2018) or singularly to contain an individual's home range (McCauley *et al.*, 2015); and, are predicted to lose climate 'baseline' conditions over the next few decades as thermoclines shift (Ackerly *et al.*, 2010; Fredston-Hermann *et al.*, 2018).

Some suggest, despite these shortfalls, that protected areas can provide an 'insurance policy' to climate change (Roberts *et al.*, 2017). However, ecological surprises are still likely despite all the best insurance (Williams & Jackson, 2007; Bates *et al.*, 2017). For example, a hypothesised 'insurance' effect assumes that species replacement is constant, and that all regions and functional groups have the same capacity for species' turnover. Two separate findings in this thesis contradict these insurance assumptions. First, the thermal niche structure discovered in Chapter 3 implies there are uneven benefits of protected areas which depend on where species occur within their thermal niches – these benefits are also 'capped' by temperature (Waldock *et al.*, 2019). Second, response diversity can be spatially heterogeneous, which would lead to biogeographic context-dependency of protected area effects on the ecosystem functions provided by reef fish (Chapter 4, although mostly response diversity was homogenous). How biogeographic niche structure of species' assemblages may undermine a protected area's capacity to deal with large-scale and long-term stressors should be further explored (despite successes in managing stressors where ecological responses are more local, e.g., exploitation, Edgar *et al.* 2014).

6.7 Final remarks

> "*The more eyes, different eyes' we know how to bring to bear on one and the same matter, that much more complete will our "concept" of this matter, our "objectivity" be.*" – Nietzsche, 1887.

In this thesis, I have addressed knowledge gaps in how assemblages respond to heterogeneous temperature change, and in realised thermal niches structure and diversity across different systems. Refining knowledge of the factors that structure species' distributions is essential to better quantify biodiversity change. Here, I used novel statistical approaches and well-replicated surveys to quantify realised niches for whole assemblages (e.g., Chapter 3 and 4), which has remained challenging to date. Where standardised data are not available, I test the applicability of a realised niche approach at an assemblage scale (Chapter 5). Challenges remain in identifying relevant scale of investigation, and in the multifarious nature of assemblages and species' niches, which provide ample avenues of future research. Humankind's diverse impacts on the natural world demands an equally diverse research agenda – rich in theory, ideas and scale. The perspective of environmental niches discussed throughout this thesis is one approach, of many, helping enlighten us to the consequences of human actions on the natural world.

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Appendix 1 A summary of literature review methods, results, discussion, and references for Chapter 2

1.1 Method

A literature review was undertaken by searching ‘Web of Knowledge’ for studies published between 2005 and 2015, for multiple taxonomic groups (bird, mammal, plant, fish, invertebrates, insect, amphibian, reptile, marine mammal) the topic was refined to combinations of (‘climate’ OR ‘temperature’) AND (‘change’ OR ‘increase’ OR ‘variation’ OR ‘anomaly’ OR ‘extreme’ OR ‘seasonality’) with the additional search field of (‘diversity’ OR ‘biodiversity’) AND (‘response’ OR ‘change’ OR ‘loss’). A second search was undertaken using (‘climate’ NEAR (‘change’ OR ‘variability’ OR ‘velocity’)) NEAR ((alpha OR beta OR gamma) NEAR diversity). The popular search teams such as ‘climate change’ and
‘biodiversity’ resulted in a wealth of literature (n=2735) therefore, whilst community wasn’t specifically searched for (due to multiple definitions across different fields for ‘community’) the broader and more popular keyword ‘biodiversity’ encompassed most relevant ecological studies of communities. Additional relevant literature was identified from the reference lists from the retrieved studies. From this literature search articles were removed if they did not fit the following criteria: (i) linking change in temperature parameters to community response (not population, individual or species level), (ii) observational studies should be recent influence of temperature change (<150 years) rather than over geological time frames, (iii) temperature parameter should be considered as driving a temporal change in communities. This resulted in 156 peer-reviewed articles from which study attributes were determined to understand current coverage of temperature dimensions in the literature. We recorded the dimensions of temperature used in analyses (based on our glossary definitions in the main manuscript), taxonomic scope, research method (observation, experiment or model), and community response measured to assess research coverage over the past decade.

1.2 Review discussion

We identified 156 relevant peer-reviewed articles, from a total of 2735 articles, that were returned from Web of Knowledge searches. To reiterate from the main paper, from the 156 papers returned from our literature review we find that 86% focus on temperature magnitude, and a tiny proportion of studies investigate spatial position (3%) and availability (1%) or temporal position (4%) and availability (6%, figure 2 main manuscript). Of the metrics used to measure magnitude - the statistical distribution of temperature change - mean changes were investigated in 48% studies, and 41% of studies focussed on minimum or maximum temperatures (figure S1a). These biases show little sign of lessening through time (figure S1b).

We also find significant information gaps. Most of the returned literature focussed on a few well-studied taxonomic groups (plants, 39%; marine fishes, 20%; birds, 17%). Some charismatic groups (mammals, 1%) and functionally important taxa are highly under-represented (e.g., phytoplankton, <1%; insects, 7%). In addition to taxonomic gaps, there is limited application of different community metrics to quantify community responses to temperature change. Generally, metrics such as species richness (36%), species identity (13%) and species relative abundance (6%) are frequently used, while phylogenetic metrics (<1%) remain poorly examined (supplemental materials figure S1c). Diversity metrics, which are known to provide insensitive estimates of temporal community changes (Magurran and Henderson 2010), are commonly selected as a response metric (17%).

1.2.1 Magnitude: Mean temperature

In reviewing the literature, we find that changes in mean temperature predict changes in composition of fish communities (Bates et al. 2014, Magurran et al. 2015), as well as birds, plants, and invertebrates (Roth et al. 2014). Compositional responses to mean temperature are as expected when selection alters species relative abundance in a deterministic manner. A commonly documented response to warming was an increase in communities' average temperature-affinity (Community Temperature Index, CTI), across broad variety of taxa and habitats (e.g. Devictor et al. 2012, Bates et al. 2014, Duque et al. 2015, Gaüzère et al. 2015, Tayleur et al. 2015). The link between temperature and community warming, measured using the realized niche, supports the expected role of selection community processes filtering for warm-adapted species, which in turn drives trends in community composition in response to average temperature conditions.

In contrast to composition and trait-based community changes, evidence for species richness being tightly linked to mean temperatures is weaker. For example, the direction of change in richness with warming is variable, with frequent documentation of no effects (Menéndez et al. 2006, Magurran et al. 2015, Tayleur et al. 2015) and positive effects (Hiddink and ter Hofstede 2008, Davey et al. 2012).

1.2.2 Magnitude: Extreme events

Extreme events are defined by statistically extreme and temporally abrupt periods of temperature, relative to the temperature variability experienced over an organism's life-cycle. These discrete events often have disproportional effects on organisms relative to the duration of the event and the effects of an underlying long-term trend in temperature (Jentsch et al. 2007, Smith 2011, Bailey and van de Pol 2015). Variation in the inherent sensitivity of communities, in combination with the short and infrequent nature of such events, means that predicting and measuring the impact of extreme events can be challenging (Smith 2011). At a population level, temperature extremes have been generally shown to cause drastic abundance declines of species' populations (between 13% to 19% decline in bird abundances, Albright et al. 2010; 100% cover reduction in macroalgae, Smale and Wernberg 2013. The effects are worsened in regionally extensive extreme events, such as the European 2003 heatwave, where movement cannot facilitate avoidance of physiological damaging temperatures. In these events, mortality and demographic changes are extreme (Jiguet et al. 2006, Garrabou et al. 2009), particularly for sessile species (Mouthon and Daufresne 2006).

Community relative abundance responses to extreme events are much more responsive than richness changes in bird species across the USA (Albright et al. 2011). In contrast, large scale richness losses were found for freshwater molluscs when abundance declines are high enough to causing local extinctions, because of limited movement capability relative to the duration of the extreme event in this taxa (Mouthon and Daufresne 2006). Species' abundance changes are generally directional with respect to thermal affinity (Day et al., Jiguet et al. 2006, Boucek and Rehage 2014, Wernberg et al. 2016), and can have drastic impacts on ecosystem structure and services beyond the community scale effects ((Pratchett et al. 2011, Butt et al. 2015, Wernberg et al. 2016)). However, community responses vary greatly between studies, which is expected because community responses to extreme events depend on: i) how extreme events alter species interactions (Butt et al. 2015), ii) historical contingencies in community composition prior to extreme events (i.e., priority effects), iii) and post-disturbance chance colonisations post-extreme events (i.e., ecological legacy effects, Seifert et al. 2015).

1.2.3 Temporal availability and position

At a species level, responses to the temporal dimensions of temperature change are frequently documented but our review demonstrates that evidence is limited for community-scale responses. Meta-analyses of species-level responses to temperature timing suggest widespread earlier timing of life-history events, migration, and date of emergence in marine (4.4 days per decade, Poloczanska et al. 2013) and terrestrial (2.3-2.8 days per decade, Parmesan and Yohe 2003) systems. We found only one observational study of whole community responses to temporal position of temperature change, Thomsen et al. 2015). In this study, advancing species abundance is linked to species thermal tolerance limits, highlighting a role for selection processes driving community compositional responses. This effect occurs because timing affects fitness peaks throughout the year which depends on species thermal preferences.

1.2.4 Availability

Our review suggests that when quantifying community responses to changes in temperature availability across space, even a basic foundation is lacking Our review suggests few, if any, observational studies exist that document regional or local community responses to recent changes in temperature availability (i.e., novel climates, changing size and shape of preferred temperatures). This is an important knowledge gap given that from 4% to 20% of the Earth's terrestrial surface is expected to be affected by changing temperature availability by 2100 (specifically novel climates, Williams and Jackson 2007). Multi-species distribution models and theoretical explorations have, however, identified a role of emerging novel temperature regimes in driving community turnover through new species groups assembling in this novel temperature niche space (Stralberg et al. 2009).

1.2.5 Position

Indicative of species' movements being an essential process driving richness gains, projections from species distribution shifts in birds suggest species richness gains will occur across the United States of America (Bateman et al. 2016). In contrast, historic high rates of forward velocity after the last glacial maximum (i.e., the distance to suitable sites post-warming) were not perfectly tracked by species movements. This inability to track change in the spatial position of temperature likely explains local extinctions, particularly for species with small ranges and endemics, in climatically unstable regions, contributing to latitudinal variation in species richness (Sandel et al. 2011). Data from contemporary biological communities suggest species movements may lag behind the rate of temperature velocity (perhaps due to spatial variation in temperature leading to climate refugia and slowing responses to the position dimension of temperature change). For example, across a range of terrestrial taxa, the average thermal affinity of species in a community (CTI) increases directionally with temperature velocity, but at a slower rate than necessary to maintain constant temperatures (Devictor et al. 2008, 2012).

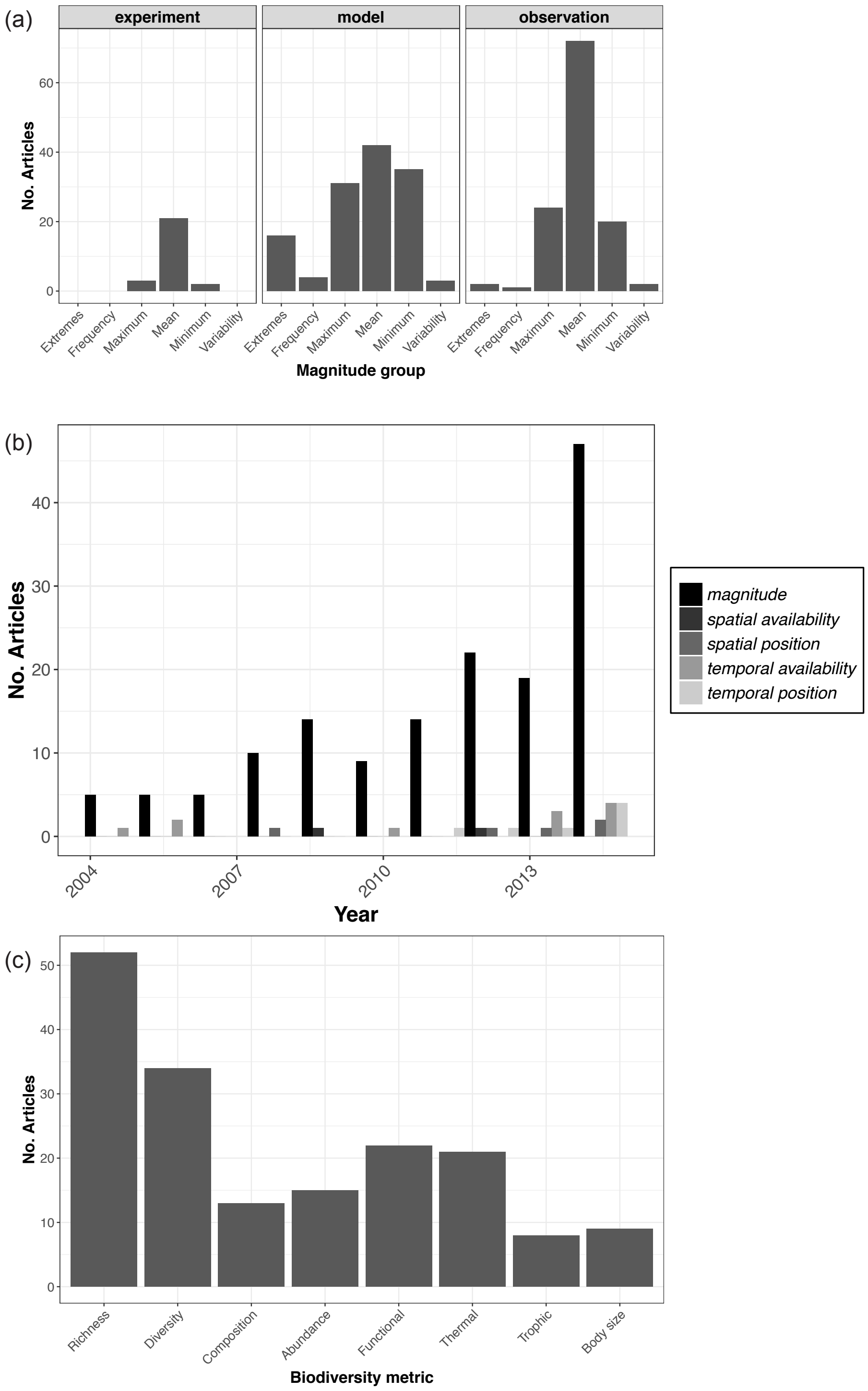

Figure S1. Summary plots from literature review. (b) Aspects of magnitude dimension studied in explaining community responses. (c) Metrics commonly used to study observational responses to temperature change, richness-based metrics are most common. Number of articles published for each dimension and year across all dimensions.

1.3 Review articles

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Appendix 2 Supporting methods for Chapter 3

2.1 Confidence scoring species thermal distribution

We apply a semi-quantitative confidence scoring system to obtain a test set of ‘high confidence’ species to ensure our results are robust the limited extent and coverage of observational data. Overall, these results have little qualitative influence on our results, and our analyses are to all intents and purposes identical if we do, or do not, filter ‘low confidence’ species. All species have at least 30 abundance records and samples that cover 3°C in any of our analyses. In addition, we assign a confidence score of 3 and remove points if the criteria in Table 1 are violated. 181 species had a score of 3; 330 a score of 2; 178 a score of 1 and 13 a score of 0. When modelling using species’ distribution model defined T_{skew} values (i.e., T_{min} and T_{max} are estimated from SDMs rather than observed thermal limits), we apply addition confidence criteria in Table 2. For these species 99 had a score of 3; 225 a score of 2; 233 a score of 1 and 115 a score of 0 or less.

Table S1. Confidence scoring criteria applied to ensure results are robust to the following limitations in using observational data.

Criteria	Score deduction	Justification
>10 absences beyond sampling thermal limits	-1	Avoids estimation of realised limits when sampling does not capture range edge
Deviance explained by quantile gam is > 75th quantile of deviance explained across all species	-1	Subsets to the most predictive abundance models
Standard deviation in estimates of T_{opt}, due to bootstrapping, is not > 0.5	-1	Avoids T_{opts} with high uncertainty
T_{opt} does not buffer sampling limits	-1	Avoids extrapolation of T_{opt} to beyond sampled temperatures
T_{opt} does not buffer T_{max} or T_{min}	-1	Avoids extrapolation of T_{opt} to beyond sampled temperatures

Table S2. Additional confidence scoring criteria applied to SDM model estimated realised thermal niche edges to ensure results are robust to the following limitations in using model derived niche edges.

Criteria	Score deduction	Justification
T_{max} or T_{min} are 3°C above or below sampling limit	-1	Avoids extrapolation beyond sampling limits
Specificity or sensitivity from species distribution model is < 0.7	-1	Reduce confidence where thermal limit is poorly predicted
Range of temperatures between T_{min} and T_{max} is not 0.5 – 2x the sampling range	-1	Avoids over or under-prediction of thermal range sizes

2.2 Deriving T_{min} and T_{max} using species' distribution models

To estimate T_{min} and T_{max} we first estimated geographic distributions from an ensemble of 5 species distribution models (SDMs) fitted in the R package 'sdm' independently for each species (Naimi and Araújo 2016). For each species we fitted SDMs using five methods: boosted regression trees, generalized additive models, generalized linear models, supported vector machines, random forests. These approaches are a combination of approaches with high expressiveness and insensitivity to correlated covariates (e.g., random forests) with those that create general functional forms (e.g., generalized linear models), we chose approaches best suited to true presence-absence data rather than approaches optimised for pseudo-absences (Elith and others 2006, Guillera-Arroita et al. 2015). We predicted occupancy probabilities from an ensemble of models, which leads to higher accuracy compared to relying on any single underlying model (Araújo and New 2007, Marmion et al. 2009).

We aimed to maximise the predictive capacity of our SDMs by including 15 variables (Table S3) expected to influence species' occupancy rates through effects on: organism physiology (temperature, pH, oxygen), resource availability (primary productivity, nutrient supply), dispersal and establishment capacity of larvae (current velocity and wave strength), exploitation (human population density) and geographic and bathymetric effects (depth, reef area, distance to land). To remove the potential influence of multicollinearity we reduce the dimensionality of our covariate set for each species using PCA, as before we only include axis with > 10% explained variation. Covariate data were upscaled into ~0.08° grids to match spatial resolutions across various data sources. Exploring the influence of each covariate is beyond the aims and scope of this study, we instead estimate the combined effects of all covariates on species' geographic distributions to obtain more accurate estimates of the realised thermal limits than from thermal limits observed from known survey locations alone.

The accuracy of each species SDMs was evaluated by averaging AUC, specificity (1 - false-presence rate) and sensitivity (1 - false-absence rate), and true-skill (TSS = sensitivity + specificity - 1) statistics across 5-fold cross validations (Fig. S6). Models had good predictive ability with AUC scores of 0.79 ± 0.08, TSS scores of 0.55 ± 0.13. Model ensemble occupancy probabilities were weighted by AUC scores of independent model runs, Whilst AUC statistics can be misleading and confound SDM sensitivity and specificity (Lobo et al. 2008), they are a useful and simple approximation of model predictive accuracy commonly applied to macroecological applications of species distribution models (Visconti et al. 2016, Newbold 2018). We rescaled probabilities of species' occupancy to 0-1 range to ensure probabilities are standardised between species (i.e., some species are naturally more frequent or rare). We next exclude all cells with a value of < 0.1 and estimated the upper and lower thermal edges of species' distributions as the 5th and 95th quantiles of temperature within this relative probability range (estimates of T_{min} and T_{max} were highly correlated regardless of this occupancy threshold, Fig S7).

2.3 Literature cited

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Appendix 3 Additional figures and tables for Chapter 3

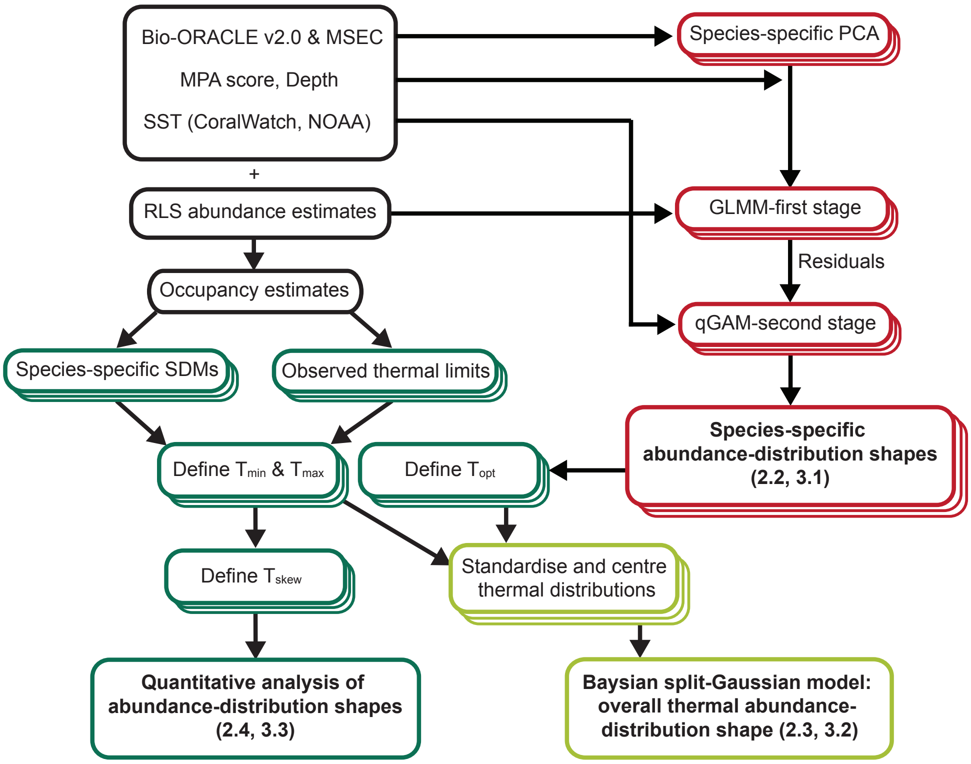


Figure S1. Schematic diagram outlining data and analyses used in the manuscript. Section numbers are provided in parentheses. Stacked nodes indicate each species is treated independently.

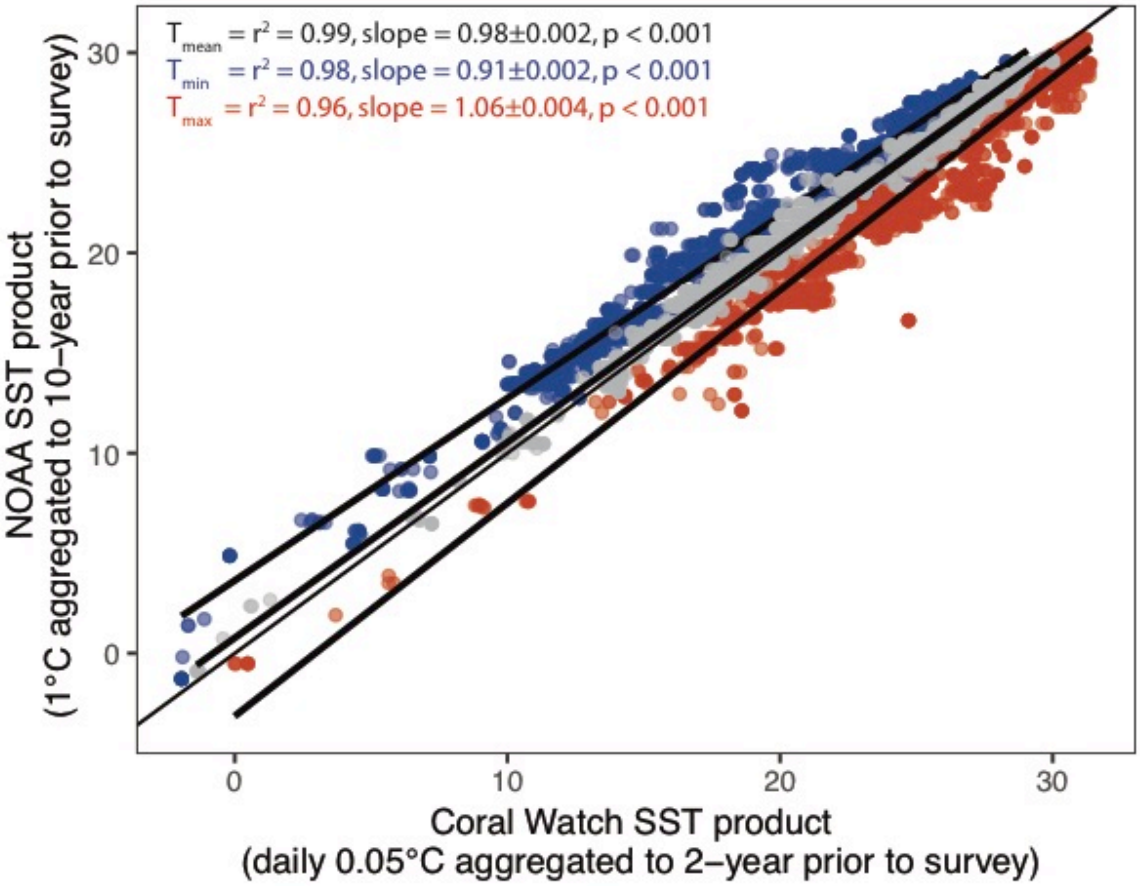


Figure S2. Comparison between satellite sea surface temperatures (SST) for high resolution (Coral Reef Watch) and lower resolution (y-axis, NOAA OI SST V2) data products. Coral Reef Watch data are aggregated to 2 years prior to Reef Life Survey samples, and NOAA OI SST V2 data are aggregated to 10 years prior to Reef Life Survey samples. Mean SST is almost identical between at an RLS site scale for displaying an almost 1:1 relationship. There is also extremely high amount of shared variation between data sources when comparing minimum and maximum temperature to NOAA OI SST mean.

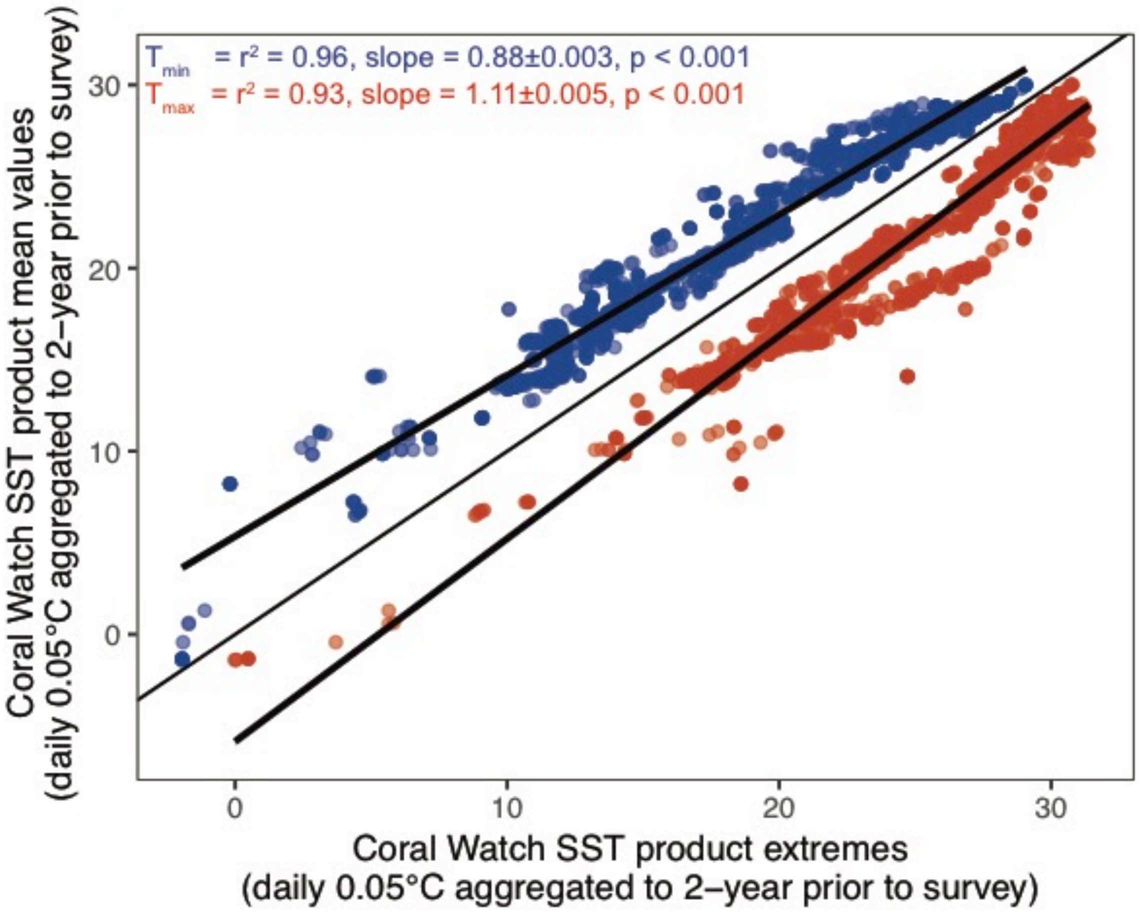


Figure S3. Coral Reef Watch SST product mean values compared to extremes. Very little variation in maximum or minimum temperatures is independent of mean temperature, such that modelling with the mean is adequate to capture the main source of temperature variation across species' geographic ranges, that is, latitudinal variation in temperatures rather than local to regional features such as ocean upwellings or currents.

Appendix 3

Table S1. Covariate data obtain from MSEC and Bio-ORACLE v2.0 for use in modelling abundance. PCA were estimated for gridded variables only, all variables other than temperature were included in GLMMs prior to fitting quantile model between temperature and local abundance.

Variable name	Unit	Source and reference	Spatial scale	PCA
Depth	m	RLS surveys	Survey	
MPA status	NEOLI score	RLS surveys (Edgar et al. 2014)	Survey	
Human population density	individuals	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)	X
Net primary productivity	mg C m^{-2} day^{-1}	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)	X
Reef area in $15km^2$ (where applicable)	km^2	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)	X
Current velocity (mean)	M s^{-1}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Current velocity (max)	M s^{-1}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Dissolved oxygen (min monthly)	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Iron	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
pH	NA	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Phosphate	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Salinity	PSS	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Silicate	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)	X
Temperature	°C	NOAA Coral Reef Watch	2.5 arc-minute (~4.6km)	

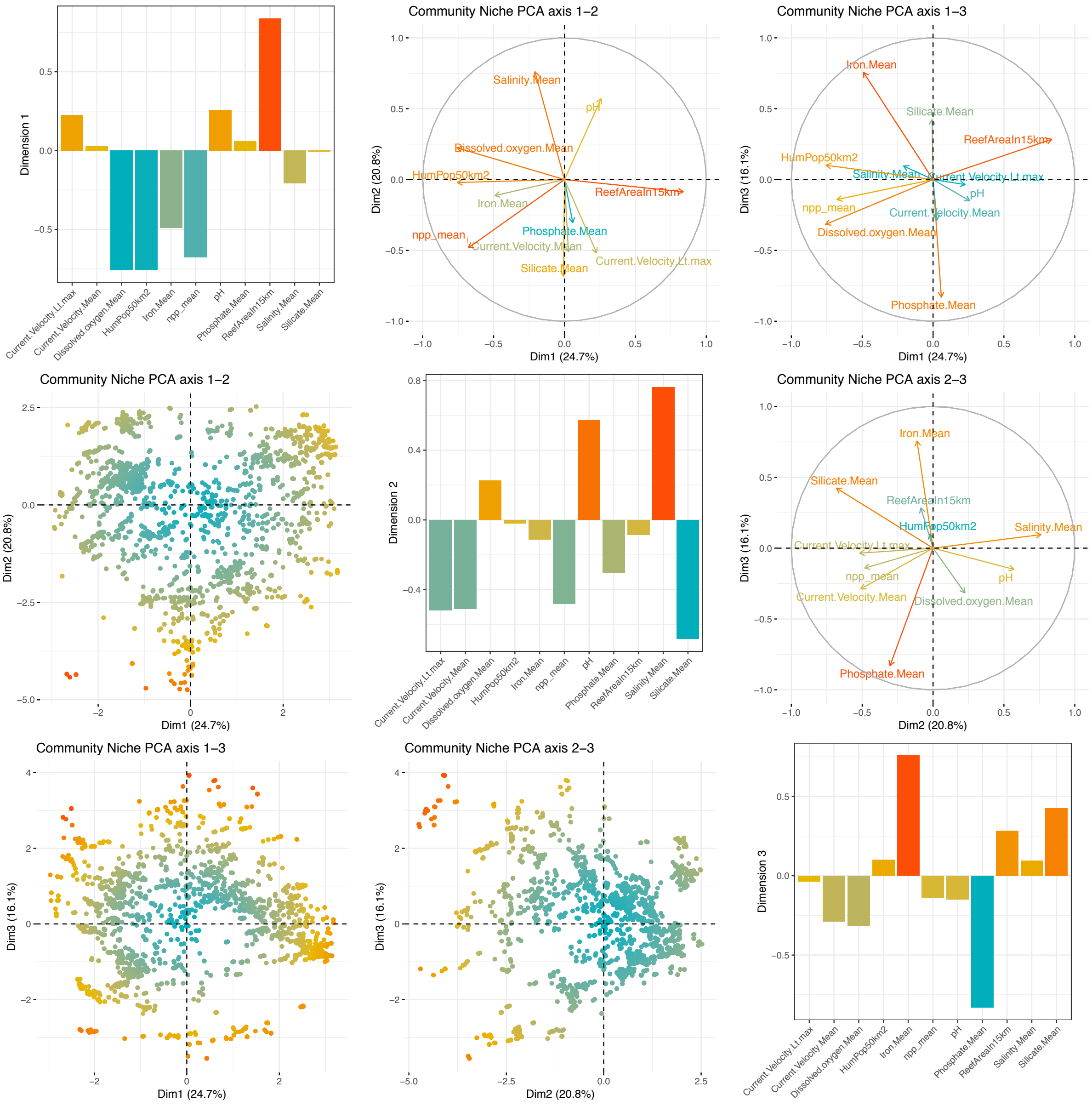


Figure S4. Principal component analysis top 3 PCA axis which together explain 61% of variation in 11 covariates across all RLS sites together. The major axis of variation here are low nutrient isolated reef systems far from human populations (PC1, 25%), high salinity, high pH, low silicate systems (PC2, 21%) and high iron, low phosphate systems (PC3, 16%).

Table S2. Prior distributions used in JAGS thermal performance curve model, section 2.3.

Parameter	Prior	Limits
T_{opt}	dnorm(0, 0.001)	
σ_{Tmin}	duniform(0, 10)	
σ_{Tmax}	duniform(0, 10)	
c	dnorm(1, 0.001)	0-1

Table S3. Covariate data obtain from MSEC and Bio-ORACLE v2.0 for use in species' distribution models to define T_{min} and T_{min}.

Variable name	Unit	Source and reference	Original spatial scale
Depth	m	GEBCO version 20150318, Weatherall et al. (2015)	30 arc-second (~1km)
Land area in 50km^2	km^2	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)
Human population density	individuals	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)
Net primary productivity	mg C m^{-2} day^{-1}	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)
Reef area in 15km^2 (where applicable)	km^2	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)
Wave energy flux	kW m-1	MSEC, Yeager et al. (2017)	2.5 arc-minute (~4.6km)
Current velocity	M s^{-1}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Dissolved oxygen (min monthly)	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Nitrate	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Iron	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
pH	NA	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Phosphate	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Salinity	PSS	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Silicate	mmol m^{-3}	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)
Temperature	°C	Bio-ORACLE v2.0, Assis et al. (2018)	5 arc-minute ~(9.2 km)

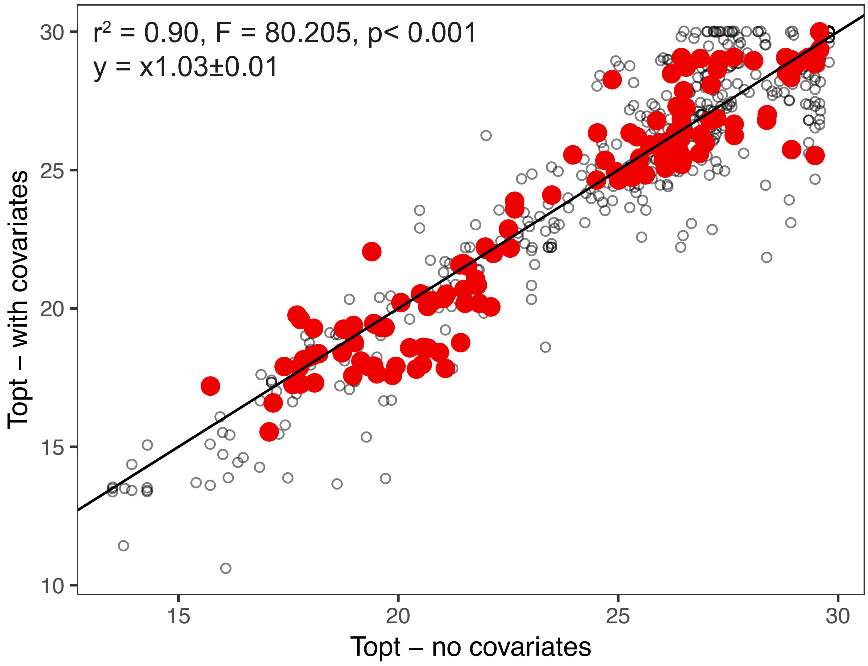


Figure S5. Comparison of T_{opt} values where covariates are included and excluded in model fits (note T_{opt} values without covariates also have coarser 1° x 1° temperature data from preliminary models). Red points indicate high-confidence species.

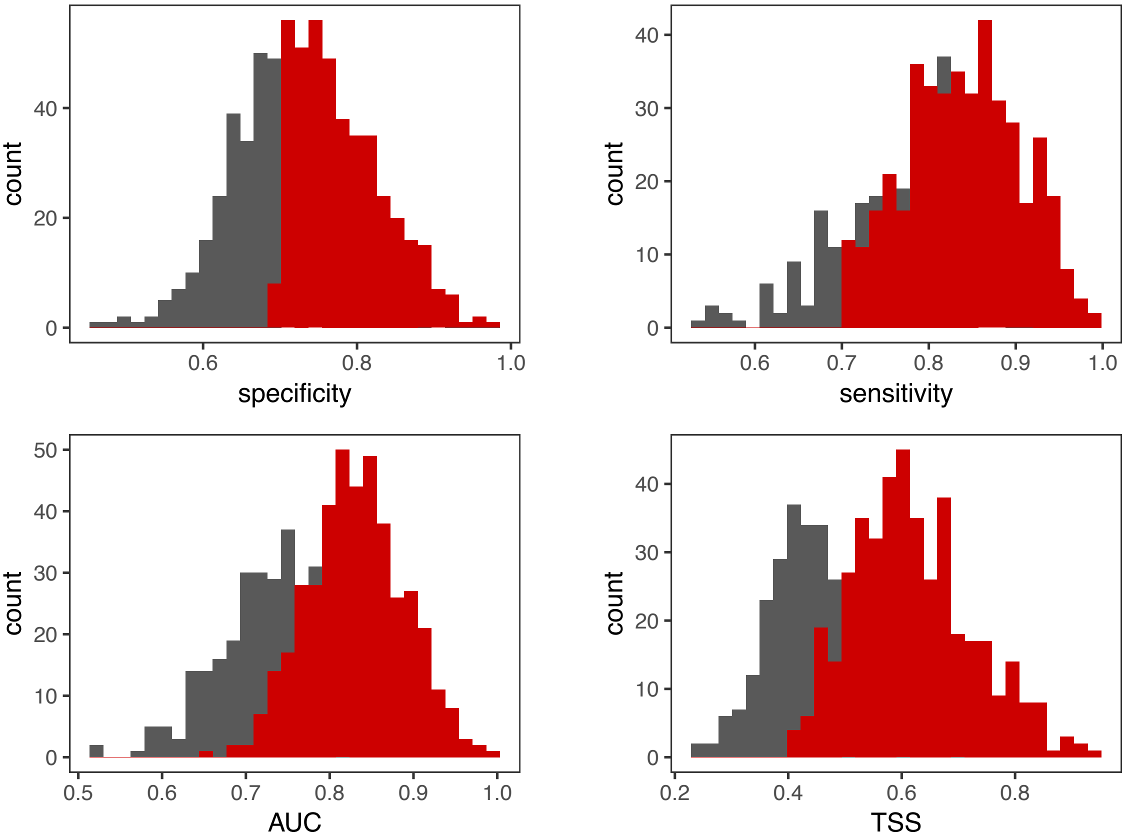


Figure S6. Metrics of species distribution model performances. Stacked histograms showing specificity (presence rate), sensitivity (absence rate), area under the receiver operator curve (AUC) and true-skill statistic (sensitivity + specificity – 1). Red bars represent a 'high-confidence' subset criteria where specificity and sensitivity are > 0.7 and grey bars represent all remaining species.

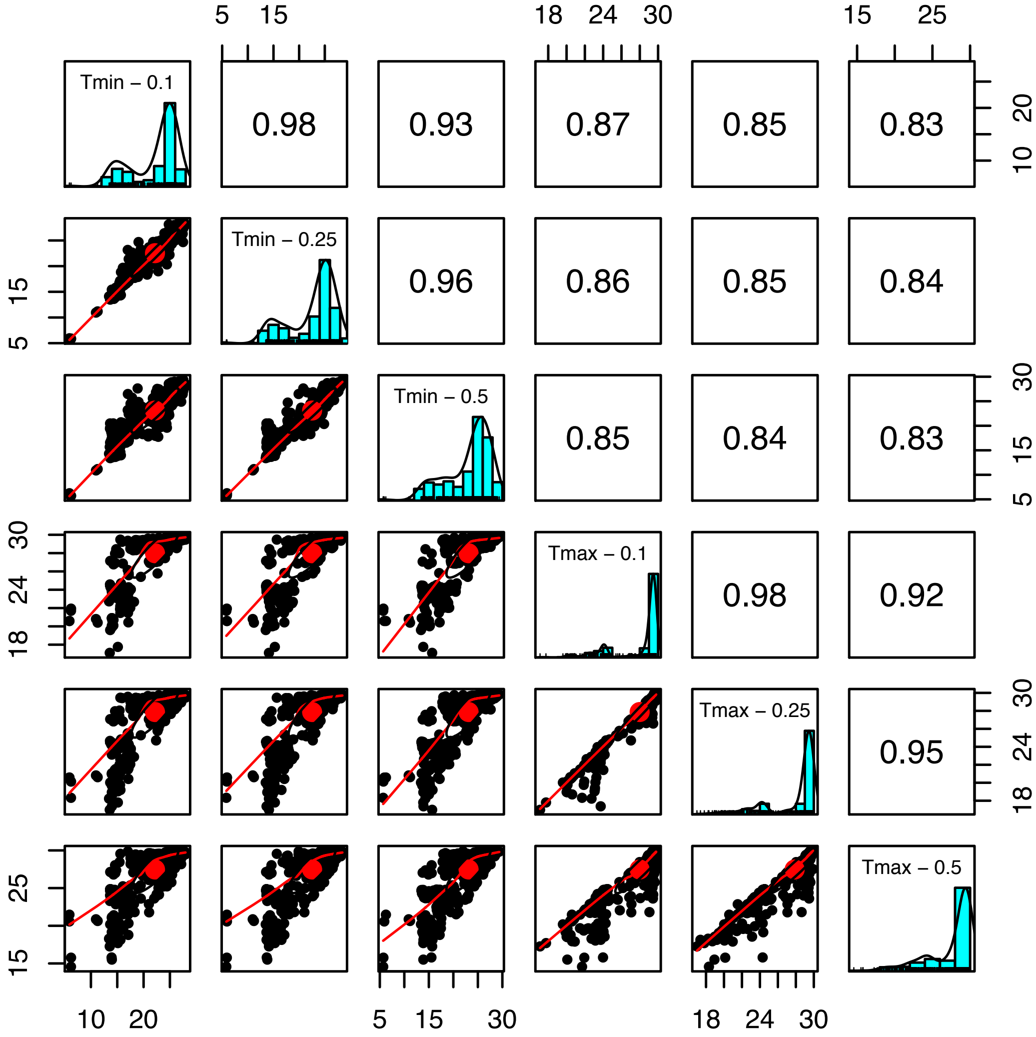


Figure S7. Pairwise correlations between T_{min} and T_{max} estimated based on different threshold values in species distribution models.

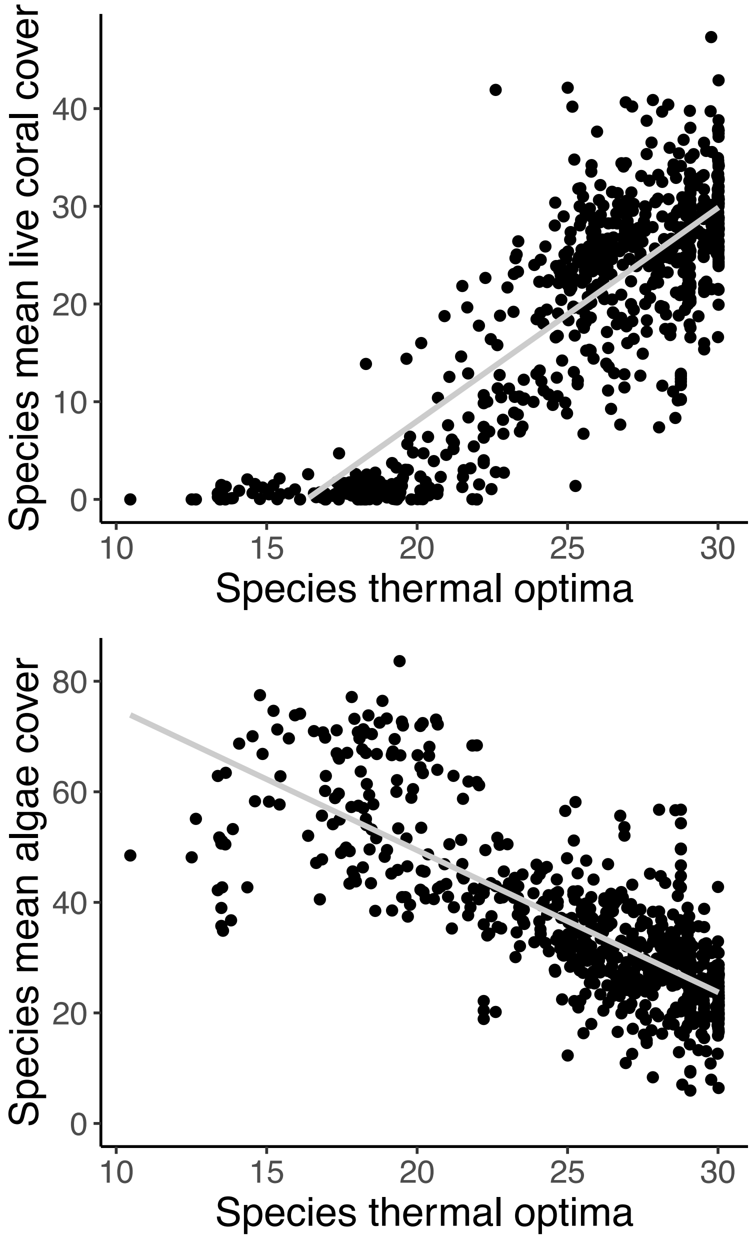


Figure S8. Correlations between T_{opt} and species coral and algae association.

Table S4. Coefficient summary tables for models predicting T_{skew} including all species. Models are fit to T_{skew} defined in three ways, from observed thermal distribution limits, from observed thermal distribution limits which include seasonality, and from species' distribution models (see methods). Models are fit separately for tropical and temperate species, tropical-2 refers to tropical species with T_{opt} less than the median T_{opt} and all tropical species. Note:*p<0.05; **p<0.01; ***p<0.001.

	T-skew								
	Observed			Seasonal			SDM		
	Tropical	Temperate	Tropical-2	Tropical	Temperate	Tropical-2	Tropical	Temperate	Tropical-2
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
T-opt	-0.64***	-0.40***	-0.57***	-0.78***	-0.50***	-0.61***	-0.65***	-0.48***	-0.52*
	(0.02)	(0.04)	(0.05)	(0.02)	(0.04)	(0.05)	(0.08)	(0.10)	(0.24)
Coral association	0.03***	0.11***	0.01	0.05***	0.13***	0.03**	0.07*	0.20	0.15*
	(0.01)	(0.02)	(0.01)	(0.01)	(0.02)	(0.01)	(0.03)	(0.13)	(0.06)
Algae association	-0.01	-0.03***	-0.01	-0.01	-0.03***	-0.004	-0.01	-0.03	-0.06
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.03)	(0.02)	(0.05)
Intercept	15.63***	9.54***	14.51***	18.26***	10.90***	14.13***	15.44***	11.36***	12.48
	(0.77)	(0.79)	(1.46)	(0.75)	(0.79)	(1.32)	(2.80)	(1.91)	(6.63)
Observations	524	177	262	524	177	262	74	25	32
Log Likelihood	-668.29	-278.43	-351.84	-657.21	-278.94	-323.40	-113.31	-35.72	-53.11
Akaike Inf. Crit.	1,352.58	572.85	719.68	1,330.41	573.88	662.80	242.62	87.44	122.22
Bayesian Inf. Crit.	1,386.67	598.26	748.22	1,364.50	599.29	691.34	261.05	97.20	133.94

Table S5. Coefficient summary tables for models predicting T_{skew} including only 'high-confidence' species. Models are fit to T_{skew} defined in three ways, from observed thermal distribution limits, from observed thermal distribution limits which include seasonality, and from species' distribution models (see methods). Models are fit separately for tropical and temperate species, tropical-2 refers to tropical species with T_{opt} less than the median T_{opt} and all tropical species. Note:*p<0.05; **p<0.01; ***p<0.001.

	T-skew								
	Observed			**Seasonal**			**SDM**		
	Tropical	Temperate	Tropical-2	Tropical	Temperate	Tropical-2	Tropical	Temperate	Tropical-2
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
T-opt	-0.67^{***}	-0.43^{***}	-0.61^{***}	-0.83^{***}	-0.43^{***}	-0.74^{***}	-0.65^{***}	-0.41^{***}	-0.63^{***}
	(0.04)	(0.06)	(0.06)	(0.04)	(0.07)	(0.06)	(0.08)	(0.09)	(0.16)
Algae association	0.02	-0.04^{***}	0.04	0.001	-0.05^{***}	0.02	-0.01	-0.04^{**}	-0.03
	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)	(0.02)	(0.03)	(0.01)	(0.05)
Coral association	0.11^{***}		0.14^{***}	0.11^{***}		0.12^{***}	0.07^{*}		0.10
	(0.02)		(0.02)	(0.02)		(0.02)	(0.03)		(0.05)
Intercept	13.55^{***}	10.69^{***}	10.81^{***}	17.98^{***}	10.78^{***}	14.55^{***}	15.44^{***}	10.84^{***}	15.23^{**}
	(1.44)	(1.60)	(2.00)	(1.46)	(1.72)	(2.12)	(2.80)	(1.94)	(5.43)
Observations	130	51	65	130	51	65	74	25	39
Log Likelihood	-147.51	-73.17	-71.50	-151.09	-76.99	-75.20	-113.31	-35.67	-69.24
Akaike Inf. Crit.	311.02	160.34	159.00	318.18	167.99	166.41	242.62	85.34	154.48
Bayesian Inf. Crit.	333.96	173.87	176.40	341.12	181.51	183.80	261.05	93.87	167.79

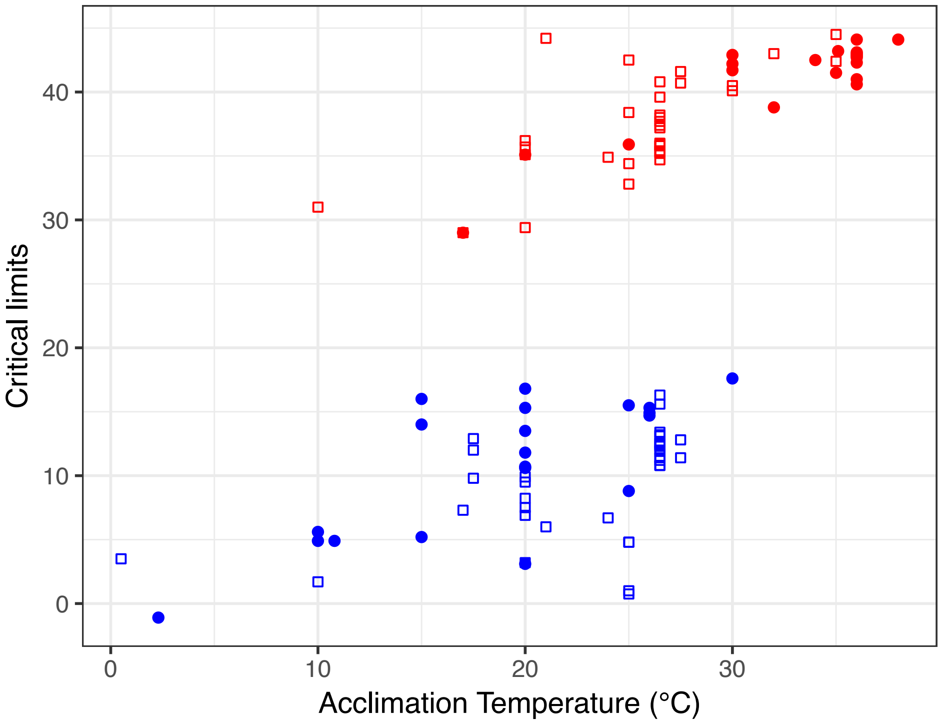


Figure S9. Upper (red) and lower (blue) critical limits for marine fish individual performance rates (various traits) across acclimation temperatures. No obvious signature of thermal guilds is present in either upper or lower limits. Data are from Sunday et al. (2011) and GlobTherm (Bennett et al. (2018) which are shown as filled circles and hollow squares, respectively. These data are the most comprehensive physiological tolerance data available which suggests that data paucity may always constrain testing thermal guild theory in physiological literature.

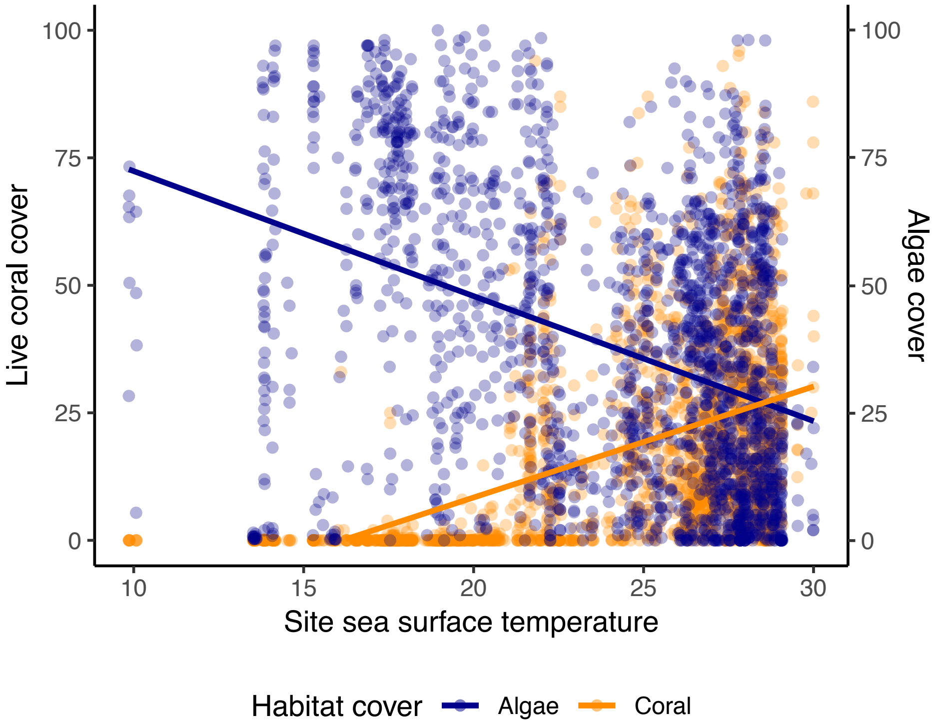


Figure S10. Relationship between algae and coral cover at all sites with site temperature. Demonstrates high levels of algae cover even in warmer waters (e.g., >25%).

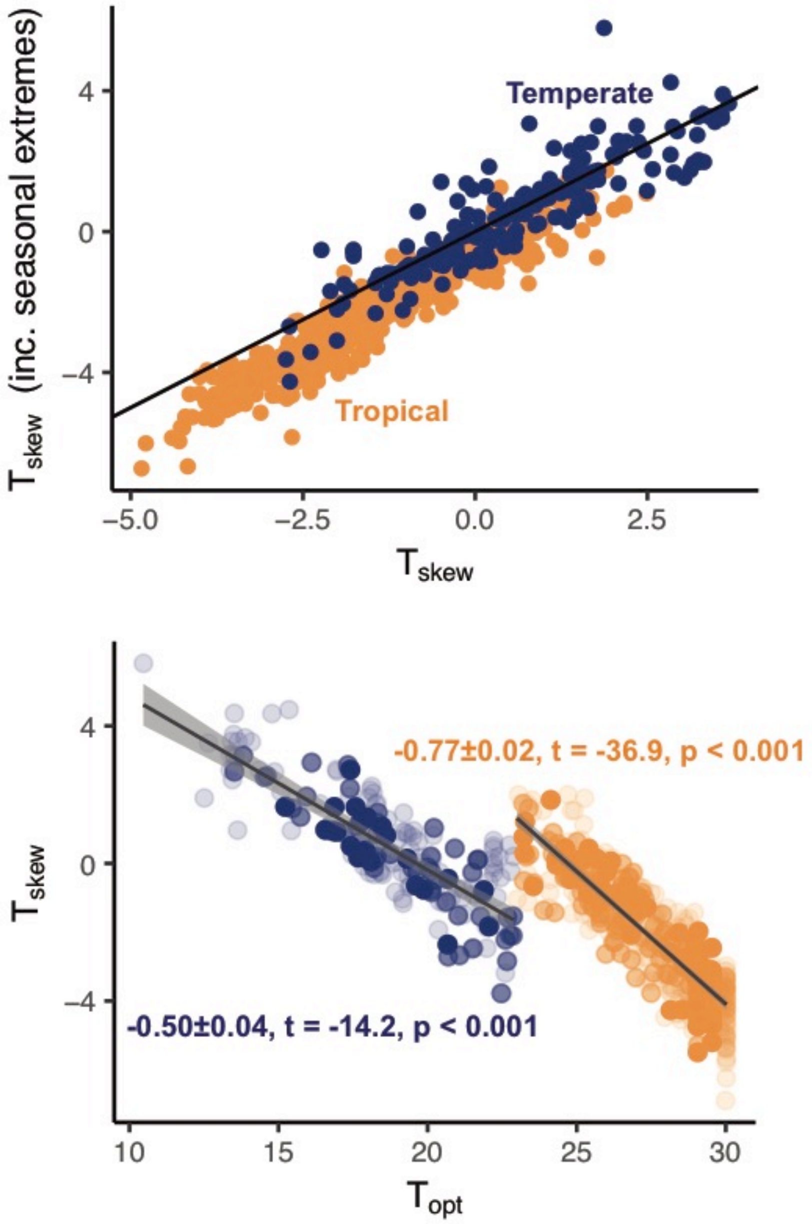


Figure S11. Comparson of main T_{skew} results (i.e., Fig 5) when T_{min} and T_{max} when estimated as the 95th quantiles of minimum and maximum temperature within a 2-year period prior to sampling. Top panel shows T_{skew} excluding seasonal variaiton compared to T_{skew} including seasonal variation which show a strongly positive slope in both temperature and tropical species, black line represents a 1:1 line. Bottom panel shows Tskew vs. Topt as in Fig 5b.

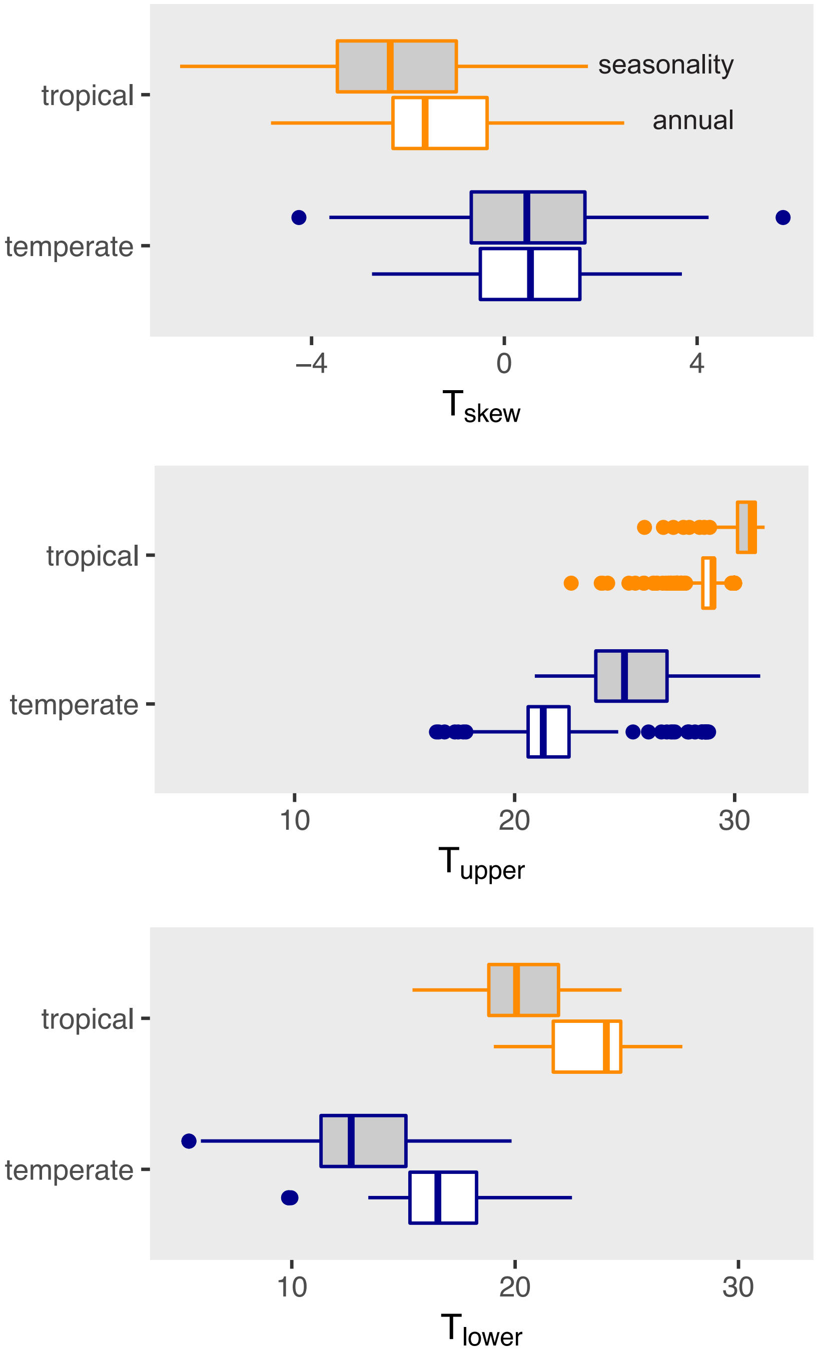


Figure S12. Comparison of T_{skew}, T_{min} and T_{max} when estimate with seasonality (filled gray) and non-seasonality (filled white) included in the estimation of upper and lower thermal niche edges for tropical (orange) and temperate (blue) species. There is a systematic broadening of species' niches, moreso in the tropical species (as in Stuart-Smith et al. 2017), but because this is balanced between upper and lower niche edges in each guild it does not strongly influence the skew of species thermal-abundance distributions.

Appendix 4 Additional figures and tables for Chapter 5

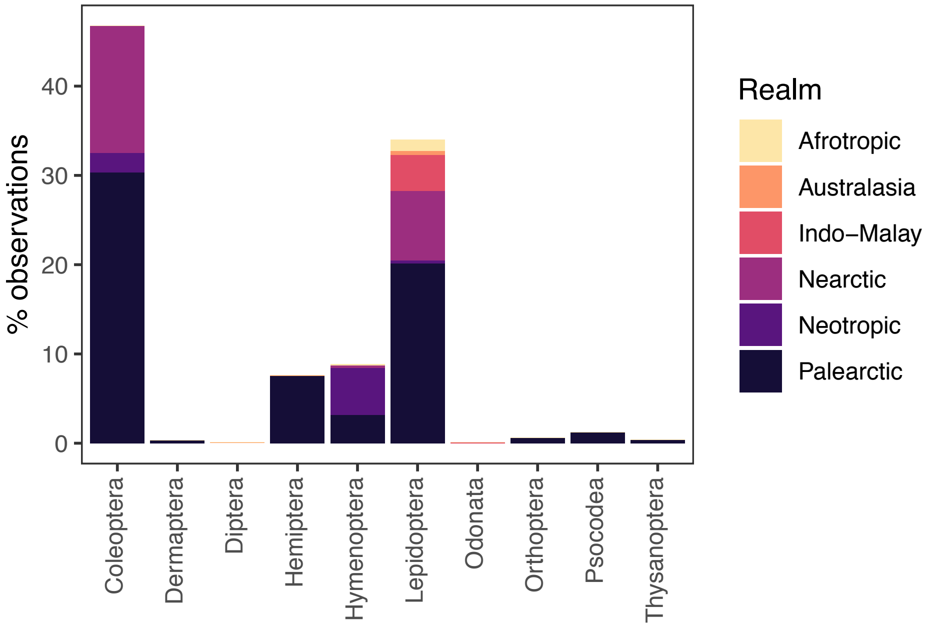


Figure S1. Class and realm breakdown as a percentage of total observations (one observation is a species presence/absence at a site).

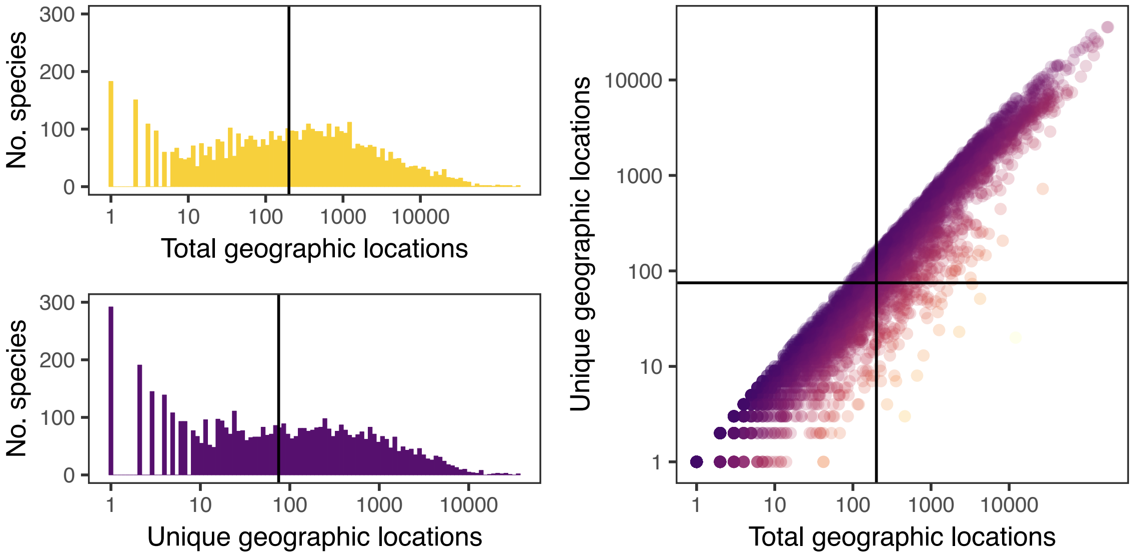
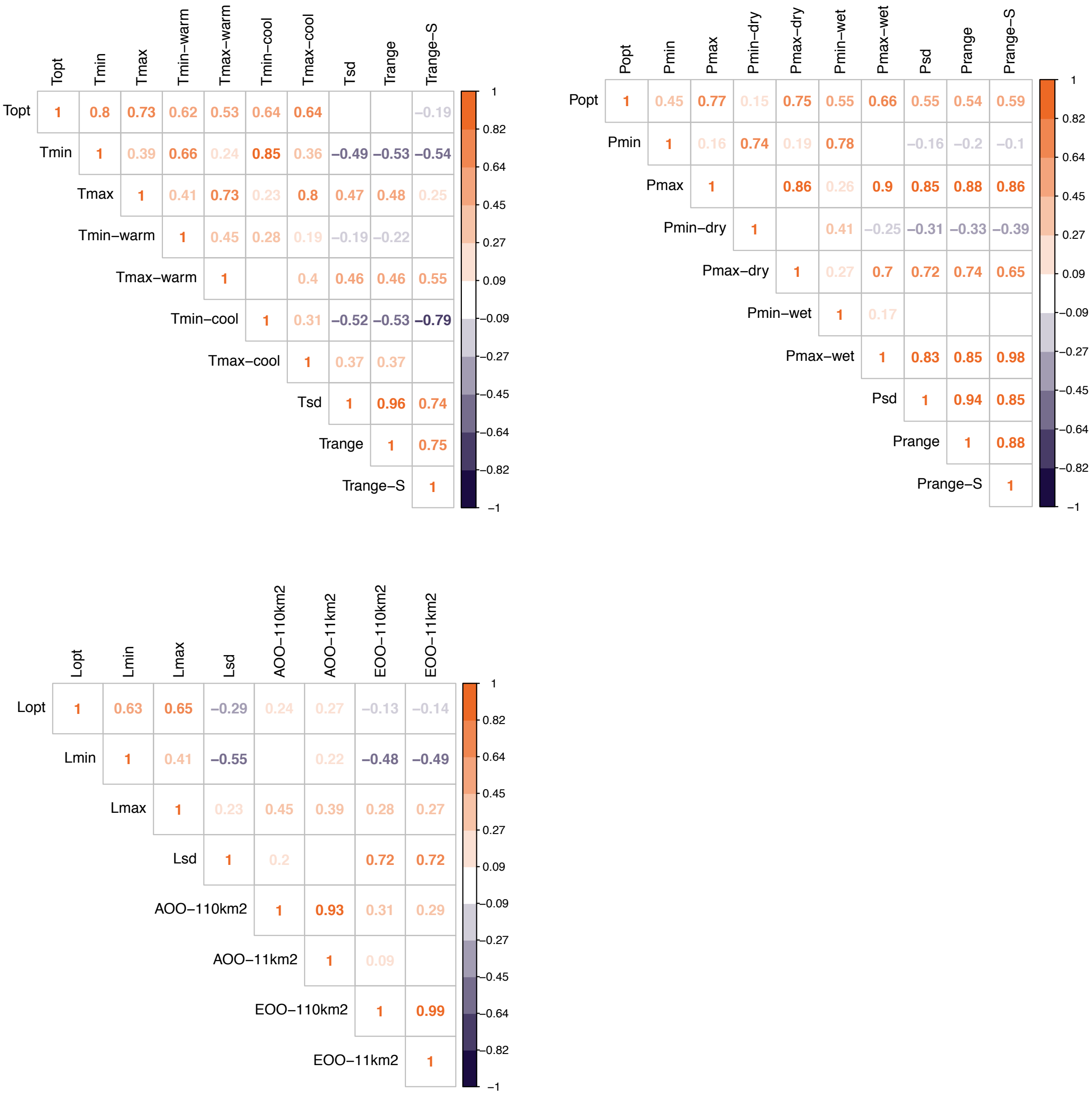


Figure S2. Comparison total number of occurrences from GBIF with number of occurrences formed from unique latitude and longitudes at within 0.01° for all insect species in the full PREDICTs dataset extract. Histograms show that the distribution of occurrences is not strongly altered by focussing on only unique occurrence locations. The number of unique records are therefore strongly related to the number of total records, thus repeated sampling is unlikely to strongly effect our results. In the main manuscript we use species with > 20 unique records.



	Topt	Tmin	Tmax	Tmin−warm	Tmax−warm	Tmin−cool	Tmax−cool	Tsd	Trange	Trange−S
Topt	1	0.8	0.73	0.62	0.53	0.64	0.64			−0.19
Tmin		1	0.39	0.66	0.24	0.85	0.36	−0.49	−0.53	−0.54
Tmax			1	0.41	0.73	0.23	0.8	0.47	0.48	0.25
Tmin−warm				1	0.45	0.28	0.19	−0.19	−0.22	
Tmax−warm					1		0.4	0.46	0.46	0.55
Tmin−cool						1	0.31	−0.52	−0.53	−0.79
Tmax−cool							1	0.37	0.37	
Tsd								1	0.96	0.74
Trange									1	0.75
Trange−S										1

	Popt	Pmin	Pmax	Pmin−dry	Pmax−dry	Pmin−wet	Pmax−wet	Psd	Prange	Prange−S
Popt	1	0.45	0.77	0.15	0.75	0.55	0.66	0.55	0.54	0.59
Pmin		1	0.16	0.74	0.19	0.78		−0.16	−0.2	−0.1
Pmax			1		0.86	0.26	0.9	0.85	0.88	0.86
Pmin−dry				1		0.41	−0.25	−0.31	−0.33	−0.39
Pmax−dry					1	0.27	0.7	0.72	0.74	0.65
Pmin−wet						1	0.17			
Pmax−wet							1	0.83	0.85	0.98
Psd								1	0.94	0.85
Prange									1	0.88
Prange−S										1

	Lopt	Lmin	Lmax	Lsd	AOO−110km2	AOO−11km2	EOO−110km2	EOO−11km2
Lopt	1	0.63	0.65	−0.29	0.24	0.27	−0.13	−0.14
Lmin		1	0.41	−0.55		0.22	−0.48	−0.49
Lmax			1	0.23	0.45	0.39	0.28	0.27
Lsd				1	0.2		0.72	0.72
AOO−110km2					1	0.93	0.31	0.29
AOO−11km2						1	0.09	
EOO−110km2							1	0.99
EOO−11km2								1

Figure S3. Pearson correlations between all variables for (a) temperature, (b) precipitation, (c) geographic distributions. Each variable is rescaled within studies; consequently, correlations amongst variables are often weak and thus amenable to multiple regression.

Table S1. Summary table for models fit independently to each trait-environment interaction term within each metric group. Metric column represents the trait used in a land-use by trait interactions (i.e., trait-environment interaction). Significant trait-environment interactions are in bold, and terms carried over into multiple regressions are in red. I carry over AOO_{110} despite statistically unclear result to provide a comparison of relative effect. Coef. represents the difference in slopes for each metric between primary forest and human-dominated land-use types with associated standard errors. X^2 and *p*-values are derived from likelihood ratio-tests with 1 degree of freedom. Delta-AIC values compares models including and excluding trait-environment interaction terms for each metric.

Group	**Metric**	**Coef.**	**se**	**X^2 (1 d.f.)**	***p***	**ΔAIC**
T-location	Topt	0.13	0.16	0.60	0.438	1.39
	Tmin	-0.16	0.17	0.95	0.330	1.04
	Tmax	0.19	0.16	1.39	0.239	0.60
	Tmin-warm	-0.30	0.17	3.35	0.067	-1.35
	Tmax-warm	**0.83**	**0.16**	**26.97**	**0.000**	**-24.97**
	Tmin-cool	-0.03	0.16	0.04	0.849	1.96
	Tmax-cool	0.08	0.16	0.26	0.609	1.73
T-breadth	Tsd	0.30	0.17	3.14	0.076	-1.15
	Trange	0.32	0.17	3.75	0.053	-1.76
	Trange-s	**0.50**	**0.16**	**9.34**	**0.002**	**-7.35**
P-location	Popt	-0.21	0.16	1.81	0.178	0.18
	Pmin	**-0.56**	**0.16**	**12.12**	**0.000**	**-10.13**
	Pmax	-0.27	0.16	2.84	0.092	-0.84
	Pmin-dry	**-0.53**	**0.16**	**10.63**	**0.001**	**-8.64**
	Pmax-dry	**-0.33**	**0.16**	**4.31**	**0.038**	**-2.32**
	Pmin-wet	**-0.41**	**0.16**	**6.67**	**0.010**	**-4.68**
	Pmax-wet	-0.21	0.17	1.57	0.211	0.42
P-breadth	Psd	0.00	0.17	0.00	0.978	1.99
	Prange	0.08	0.17	0.21	0.644	1.78
	Prange-s	-0.12	0.17	0.52	0.470	1.47
G-location	**Lopt**	**-0.35**	**0.16**	**4.56**	**0.033**	**-2.57**
	Lmin	-0.29	0.16	3.24	0.072	-1.25
	Lmax	-0.02	0.16	0.01	0.918	1.98
G-breadth	Lsd	0.20	0.16	1.50	0.221	0.49
	AOO110	0.16	0.17	0.92	0.339	1.08
	AOO11	-0.01	0.17	0.01	0.936	1.99
	EOO110	0.01	0.17	0.01	0.934	1.99
	EOO11	0.00	0.17	0.00	0.988	1.99

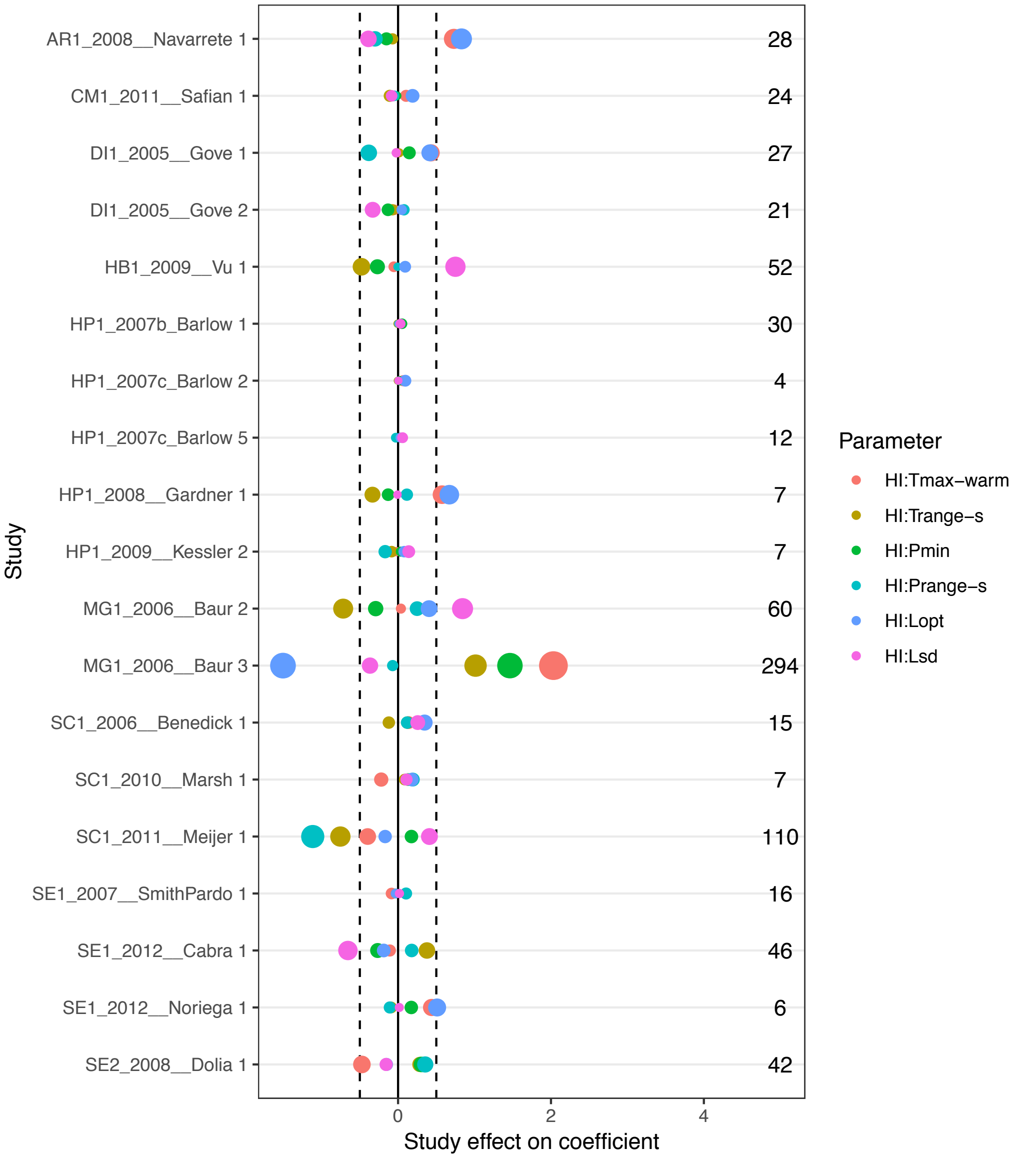


Figure S4 Difference in coefficient with study removed during sensitivity tests. Different trait-environment interactions are indicated by colours. Numbers on the right of the panel indicate the number of species per study.

Table S2. Summary table of models during sensitivity test (i.e., studies removed with Cook's distance > 1). Models are fitted independently to each trait-environment interaction term within each metric group. See Table S1 for full description.

Group	**Metric**	**Coef.**	**se**	**X^2 (1 d.f.)**	***p***	**ΔAIC**
T-location	Topt	0.07	0.16	0.21	0.650	1.79
	Tmin	-0.11	0.16	0.51	0.474	1.48
	Tmax	0.29	0.16	3.50	0.061	-1.51
	Tmin-warm	0.14	0.16	0.84	0.359	1.15
	Tmax-warm	**0.48**	**0.16**	**9.40**	**0.002**	**-7.41**
	Tmin-cool	-0.25	0.16	2.61	0.106	-0.62
	Tmax-cool	0.24	0.16	2.40	0.121	-0.41
T-breadth	Tsd	0.31	0.16	3.62	0.057	-1.63
	Trange	0.29	0.16	3.31	0.069	-1.32
	Trange-s	**0.45**	**0.16**	**8.54**	**0.003**	**-6.55**
P-location	**Popt**	**-0.70**	**0.15**	**22.02**	**0.000**	**-20.03**
	Pmin	**-0.63**	**0.16**	**16.68**	**0.000**	**-14.69**
	Pmax	**-0.49**	**0.15**	**10.10**	**0.001**	**-8.11**
	Pmin-dry	**-0.53**	**0.16**	**11.16**	**0.001**	**-9.17**
	Pmax-dry	**-0.47**	**0.15**	**9.25**	**0.002**	**-7.26**
	Pmin-wet	**-0.71**	**0.15**	**22.22**	**0.000**	**-20.23**
	Pmax-wet	**-0.35**	**0.16**	**4.94**	**0.026**	**-2.95**
P-breadth	Psd	0.02	0.16	0.01	0.919	1.98
	Prange	-0.10	0.16	0.38	0.539	1.61
	Prange-s	-0.29	0.16	3.22	0.073	-1.23
G-location	Lopt	0.01	0.16	0.01	0.930	1.98
	Lmin	0.08	0.15	0.24	0.622	1.75
	Lmax	0.30	0.15	3.77	0.052	-1.78
G-breadth	Lsd	0.16	0.16	1.01	0.315	0.98
	AOO110	**0.34**	**0.16**	**4.27**	**0.039**	**-2.27**
	AOO11	0.27	0.16	2.78	0.096	-0.79
	EOO110	0.08	0.16	0.23	0.630	1.76
	EOO11	0.07	0.16	0.20	0.654	1.79